POPULATION DYNAMICS AND SPATIAL PATTERNS OF DIPTEROCARP SEEDLINGS IN A TROPICAL RAIN FOREST

Margaret Jean Still

B. Sc. (Hons., Aberdeen)

A thesis presented for the degree of
Doctor of Philosophy at the University of Stirling

Department of Biological and Molecular Sciences
University of Stirling
1993

ABSTRACT

Population dynamics and spatial pattern of dipterocarp seedlings were investigated in lowland dipterocarp forest in Danum Valley Conservation Area, Sabah, East Malaysia. Seedlings (<10 cm gbh) were enumerated in two areas (2.0 and 0.48 ha) within the tree enumeration plots established by the University of Stirling project, and surveyed over 22 months.

Seedlings of the major canopy and emergent dipterocarps in the area were common: *Shorea johorensis* (Red Meranti); *S. argentifolia, S. leprosula, S. parvifolia* (Light Red Merantis, LRM) and *Parashorea malaanonan*, all light demanding species; *S. fallax, S. pauciflora* (Dark Red Meranti, DRM), more shade tolerant emergent species; and *Hopea nervosa, Vatica dulitensis* and *V. sarawakensis*, shade tolerant canopy species. Total seedling densities were 2000-2500 ha^{-1}.

Mortality rates varied from 0 to 16% yr^{-1} in different species, and were highest in the LRMs and lowest in the canopy species. Temporal and spatial variation in mortality rates was greatest in the LRMs. In both plots, seedling mortality rates were significantly positively correlated with basal area of conspecific trees ≥10 cm gbh.

Net growth rates were very variable, even within size classes in the same species. Median growth rates were highest in the LRMs and lowest in canopy species. Frequency distributions of growth rates were strongly leptokurtic in slow-growing species, with most seedlings having growth rates around zero, although individual seedlings could produce large increments. In fast-growing species, more seedlings achieved high growth rates. A significant proportion of seedlings suffered height loss due to falling debris, and almost half the seedlings showed evidence of previous stem damage. Large growth increments were recorded in most species in response to canopy openings, usually very small gaps caused by branch falls. Individual increments exceeded 1 m yr^{-1} in seven species.

Growth and mortality rates were significantly positively correlated across species in Plot 1, but not in Plot 2.

Seedling spatial patterns were examined in eleven species in Plot 1, and covered a wide range of degrees of aggregation. Seedlings of the light-demanding emergent species were well-distributed throughout the study area, though some showed aggregation at a small scale. DRM seedlings were strongly clumped around adult trees. Seedlings of two of the canopy species were very strongly aggregated around adult trees, while the third species, *V. sarawakensis*, had randomly distributed seedlings.

ACKNOWLEDGEMENTS

The Danum Valley Management Committee and the Socio-economic Research Unit of the Government of Malaysia granted permission to carry out this research in Sabah. I thank Dr. Clive Marsh and staff of Yayasan Sabah at the Danum Valley Field Studies Centre. Tree identifications were provided in phase 1 by E. Campbell, and in phase 2 by C. Ridsdale at the Rijksherbarium, Leiden, and by Sabah Forest Department staff.

The guidance of Dr Mike Swaine was invaluable when I began the seedling enumeration, and I have appreciated his advice and encouragement throughout. Milton and Diana Lieberman were a source of stimulating ideas, and provided the Growth Simulation program, and advised on interpretation of the results.

I am grateful for financial support from the Carnegie Trust for the Universities of Scotland, and from the Royal Society South-east Asia Rain Forest Research Committee, especially Dr. Adrian Marshall. I thank my supervisor, Dr David McC. Newbery for allowing me to draw on the tree enumeration data, and for his advice and help.

Paul Walton assisted with the seedling survey for a day or two, and he and Jon Watt entertained us with their music. The Chew family provided a welcome haven in Kota Kinabalu.

At the University of Stirling, I am grateful to Rob Marshall and Rob Isbister of the Computing Advisory Service, and Dr David Newbery for help with computing problems. Facilities were provided by the Department of Biological and Molecular Sciences.

I thank my current employers, the Macaulay Land Use Research Institute and my boss, Dr James Gauld for allowing me access to computing facilities. For the production of the thesis, I am indebted to Elizabeth Still, who typed all the tables, and Rosemary McNiven, who prepared some of the figures in Chapters 7 & 8.

Thanks go to my parents, Robert and Jean Still, for their support, and to all friends in Kippen, Stirling and Aberdeen, Stephen and Ann Newton, and especially the 'Room': Maimie Thompson, Ross Johnston and Helen Riley, whose company I have enjoyed over the years. Ross and Maimie were always on hand to help with computing queries. Special thanks to Maimie for her friendship, support and generosity.

Finally, and most of all, I thank Stuart Sutton-Jones, for his assistance in the field throughout the seedling enumeration work, and for his unfailing support and encouragement from start to finish.

SUMMARY OF CONTENTS

CONTENTS

CHAPTER 1

INTRODUCTION

1.1 REVIEW

Tropical rain forests are one of the most species rich plant communities, and explanation of the origin and maintenance of such high diversity presents a challenge to biologists. Major questions in tropical rain forest research are:

- how is such high species richness maintained?
- to what extent does species composition vary in space and over time?
- what factors influence variation in community structure and species composition in time and space?

Bearing on all three are the differences and/or similarities between species in their regeneration patterns, and rates of growth and mortality under different environmental conditions. Answers to these questions have practical applications in the management of forests. With accelerating deforestation, especially that due to logging, there is an urgent need to develop sustainable use of the remaining forest resource and to manage productively forest that has been degraded.

Two threads run through these questions:

1) the quantification and comparison of rates of growth and mortality in different species, and the reasons for variation in time and space: how and why rates change over the life of the tree, and vary with different environmental conditions. These factors play a part in determining forest structure and dynamics.

2) the spatial dynamics of regeneration: patterns of dispersion, and the interaction of seedlings and adult trees throughout the life of the tree, from seed dispersal, to seedling performance in relation to proximity of adult trees, and in turn to the probability of recruitment near parent trees.

Maintenance of species diversity: are forests equilibrium or non-equilibrium communities?

The theories seeking to explain the maintenance of species diversity fall into two groups: equilibrium and non-equilibrium theories. According to Hubbell & Foster (1986a) the distinction between equilibrium and non-equilibrium communities is whether 'species assemblages are stabilised by intrinsic biotic interactions under the given environmental regime of the site'. The non-equilibrium view is that the stabilising factors are weak or non-existent, and species abundance drifts with random immigrations and extinctions.

The classic equilibrium theory states that individual tree species are finely adapted to a particular habitat niche and co-exist as stable assemblages of co-evolved species (Ashton 1969, Tilman 1982). Each species is able to exploit the limiting resources in a way that is different enough from other species to allow its continuing existence. The origins of such high species diversity are thought to lie in the presumed great age and climatic stability of tropical rain forests has allowed species to accumulate over time, each becoming more finely adapted to a particular niche under the influence of intense competition between species (Ashton 1969). This explanation seems inadequate to explain the co-existence of many apparently similar con-generic species, exemplified by the genus *Shorea* in Borneo.

The resources to be partitioned are relatively few, and the number of available niches seems limited (Richards 1969). In the neotropics, the dependence of trees on only a few species of mycorrhizal fungi for uptake of mineral nutrients is likely to reduce competitive exclusion (Janos 1980), and is more likely to lead to competitive equivalence (Hubbell & Foster 1986a). In Malesian rain forests, many trees, including the dipterocarps, form non-specific ectomycorrhizal associations (Singh 1966, Becker 1983, Alexander *et al.* 1992). Hubbell & Foster (1986a) argue that the high niche differentiation proposed by Ashton (1969) depended on "precise and specific coevolution of competitors", necessitating that species pairs be predictably associated with each other over long periods of time. However, Hubbell & Foster's (1983) analyses of tree neighbourhoods in a 50 ha plot on Barro Colorado Island, Panama, reveal that the "biotic neighbourhood" of individual trees are very diverse, and above all, unpredictable. Pairs of species are unlikely to be neighbours consistently enough to coevolve, and therefore competition must be diffuse. Hubbell & Foster suggest that

this uncertainty would lead to "convergent generalisation": to evolution of generalised characteristics, such as shade tolerant seedlings of similar morphologies. Grubb's (1977) 'regeneration niche' hypothesis proposes that differences between species in aspects of regeneration such as flowering and fruiting times, seed dispersal, germination requirements and light requirements for germination and seedling growth promoted the coexistence of species which could have similar requirements as adults.

The co-existence of species under equilibrium models requires some form of density-dependent regulation of species abundance. Early travellers in the rain forest (eg. Alfred Russell Wallace 1878) were struck by the high species diversity and the wide spacing between trees of the same species. Aubréville (1938) and Jones (1955) observed in West African forests that in some species, juveniles of canopy species were not found below their parents. These views led Janzen (1970) and Connell (1971) to propose that such spacing between conspecific trees was maintained by strong biotic pressures which depressed recruitment and survival of seedlings below parent trees to such an extent that there was some 'minimum distance' beyond which recruitment could occur. The space around adult trees was thus available for recruitment of other species, maintaining local diversity. Janzen (1970) suggested that seed predation was the main cause, while Connell (1971) proposed that invertebrate herbivores, attracted by the adult tree, would find the surrounding conspecific seedlings more palatable. There are two components to the hypothesis. Seed and seedling mortality are predicted to be higher nearer adults of the same species: the 'distance hypothesis'; or at high densities of conspecific seedlings: the 'density hypothesis'. Since high densities of seedlings are usually found around parent trees, the two hypothesis are often jointly viewed, and tested, as an 'escape hypothesis' (Howe & Smallwood 1982), or simply the 'Janzen-Connell hypothesis'. Augspurger (1983a, 1983b) included fungal pathogens as causes of increased mortality in seedlings near parent trees.

The results from a complete enumeration of trees over 1 cm dbh in a 50 ha plot on Barro Colorado Island (BCI), Panama, showed that most tree species were clumped, few were randomly dispersed, and almost none were regularly dispersed (Hubbell & Foster 1983). This led Hubbell (1979, 1980) to challenge the theory, and concluded that such spacing between conspecific trees could not explain the co-existence of a high number of species. Becker *et al.* (1985) supported this general

conclusion, but provided evidence from computer simulation that spacing could increase the time taken for rare species to reach local extinction. (The fact that the large dipterocarps which dominate much of SE Asia's tropical rain forests often have strongly clumped distributions due to inefficient seed-dispersal seems to have been overlooked, a fact long known to foresters and botanists in the region (Ridley 1930, Poore 1968, Ashton 1969).

The 'compensatory mechanisms' hypothesis of Connell *et al.* (1984) proposes that rare species at a site are favoured over commoner species by increased rates of reproduction, survival and/or growth, compensating for the tendency of commoner species to increase at the expense of rarer species. Central to this hypothesis is that commonness or rarity of a species are local attributes and not characteristics of the species (Connell *et al.* 1984), and the compensatory mechanisms act to regulate species abundance relative to other species, and not around some equilibrium point specific to that species.

An alternative hypothesis of species co-existence is the existence of frequency-dependent recruitment fluctuations proposed by Chesson & Warner (1981). Co-existence of species is promoted by differential recruitment rates among species in response to fluctuating environmental conditions, and mediated through variation in fecundity or seedling mortality rates. Each species has a period when its recruitment exceeds the average of all other species, and recruits are 'stored' in the form of a seedling or sapling bank (Harper 1977), so that the gains made under favourable conditions are not lost. Storage is most important to species present at low density because the gains made in favourable conditions are proportionally higher. Warner & Chesson (1985) suggest that in tropical trees, massive but infrequent recruitment may contribute significantly to co-existence of species. Such mast fruiting is a characteristic feature of dipterocarps. Other species characteristics which favour co-existence under this hypothesis include low adult mortality; high fecundity; differing sensitivity of seedlings to environmental conditions, leading to varying mortality rates and 'lottery' competition for space, all features recorded in dipterocarps populations (eg. Wyatt-Smith 1958, Poore 1968, Liew & Wong 1973, Ashton 1969, 1982)

The view that tropical rain forests are stable and compositionally at equilibrium has been challenged more recently by so-called non-equilibrium views, in which species composition is thought to change gradually in space and time in a non-deterministic manner. This is implicit in Aubréville's Mosaic Theory (1938).

Local species composition is determined by unpredictable events such as tree-fall gaps, in the 'intermediate disturbance' hypothesis of Connell (1978) who withdrew his support for the Janzen-Connell hypothesis. Strong (1977) suggested that branch and tree-falls caused by heavy epiphyte loads and lianes resulted in a level of disturbance that could enhance species diversity. The 'intermediate disturbance' hypothesis (Connell 1978) can be viewed as an equilibrium theory if small-scale disturbance is a constant feature of the environment, even if disturbance events are unpredictable in time and space (Hubbell & Foster 1986a). The large literature on gaps confirms the ubiquity of gap creation in natural forests and their importance in regeneration (Webb *et al.* 1972, Hartshorn 1978, 1979, Whitmore 1982, 1984, Denslow 1980, 1987, Brokaw 1985a,b).

Generalists or specialists: how similar or different are species?

Are there groups of species with consistent, definable and different ecological traits? It is an obvious advantage for foresters if tree species can be characterised in terms of their ecological requirements for regeneration, and their responses and performance under different environmental conditions (Swaine 1989).

One readily distinguished group are pioneer species, with a well-known set of characteristics which include small seeds, high fecundity, fast growth rates and high mortality rates in the shade (Swaine & Whitmore 1988, Whitmore 1989). The remaining species, the majority in wet tropical forests, have been classified according to their regeneration requirements, as for example 'shade tolerant', 'light-demanding', or 'requiring a gap for successful regeneration' (Hartshorn 1978, Bazzaz 1984, reviewed by Denslow 1987), underlining the importance of the 'regeneration niche' (Grubb 1977) in attempts to explain species co-existence. From results of an enumeration of trees over 3 feet girth in 23 ha of lowland forest at Jengka, Peninsular Malaysia, Poore (1968) concluded that the rare species present were less tolerant of the prevailing environmental or soil conditions, were restricted to particular niches or were pioneers. They existed in a "matrix" of common, tolerant generalist species whose occurrence is determined by "chance events" of reproduction and regeneration. In dipterocarps, these chance events include irregular and unpredictable fruiting, and differing degrees of dependence on gaps to reach the canopy.

The classifications and terminology imply suites of correlated physiological and ecological traits (Clark & Clark 1992), and trade-offs are expected between the ability to persist in the understorey and to respond to canopy openings (Denslow 1980, 1987, Bazzaz 1984). In reality, there is likely to be a continuum of traits (Denslow 1980, 1987, Pickett 1983, Whitmore 1984, Lieberman *et al.* 1985a). Recently, detailed studies of seedling and sapling performance in natural forest under different microsite conditions have shown that species cannot be simply classified on the basis of the responses of their seedlings and saplings. Hubbell & Foster (1986a) studied the distribution of saplings 1-5 cm dbh in 81 species of canopy tree in the 50 ha plot on Barro Colorado Island, Panama, and found no detectable specialisation in regeneration requirements in 70% of the species; they suggested that regeneration requirements are identical in these species. Clark and Clark (1992) followed the survival, growth and microsite conditions for six years in six non-pioneer species sampled from 150 ha of rain forest at La Selva, Costa Rica. They found no evidence that these six species showed correlated life-history traits or trade-offs. Another detailed long-term study of sapling performance in a large area of forest is that of Welden *et al.* (1991). They studied recruitment, survival and growth of saplings (1-4 cm dbh) in more than 100 species of woody plant over three years in the 50 ha plot on Barro Colorado Island. Comparison was made between sapling performance in low canopy (<10 m) and high canopy (≥10 m) sites. In contrast to Clark and Clark (1992), they did distinguish 'syndromes of correlated responses' to the two canopy height sites, and found that fast growing species tended to have high mortality rates. In Penang, Malaysia, Raich & Christensen (1990) showed that the species composition of regeneration in canopy gaps was more closely related to the species composition of the surrounding closed forest than to the composition of similar-sized gaps further away. Many of the species which regenerated in gaps, also regenerated in closed forest. In the Danum Valley, Brown & Whitmore (1992) found that dipterocarp seedlings did not partition canopy gaps, and that seedling size, and not species, was the major determinant of success in canopy gaps.

These recent studies support the view that many species are generalists (Connell 1978, Hubbell 1979) within major life-history guilds (Hubbell & Foster 1986a) in their response to small-scale canopy disturbance, one of the major driving forces of forest dynamics, and set the scene for a dominant role for chance and history in determining forest composition.

Role of plot studies

The equilibrium versus non-equilibrium question cannot be answered on a local scale because the spatial scale of most studies includes only a small part of the breeding population of most species, and studies are too short to include more than a small part of the life span of trees that can live for hundreds of years. In reality, tropical forests are unlikely to be completely equilibrium or non-equilibrium communities (Hubbell 1984). Evidence can be sought on the small scale for the existence of spacing mechanisms, and inferences can be made about their effects on future species composition. The spatial pattern of regeneration can reveal the importance of biotic interactions: if there are equilibrating forces, there should be density- and/or distance-dependence reduction in reproduction and juvenile performance in common species relative to the rare ones, while if these forces are weak, then local performance will be independent of species abundance (Hubbell & Foster 1987). In a study of floristic variation within a 11.7 ha plot in Jengka Forest Reserve in Peninsular Malaysia, Ho *et al.* (1987) concluded that non-equilibrium recovery from recent catastrophe best explained the regeneration pattern of *Elateriospermum tapos*. Clark & Clark (1984) reviewed results from 24 studies of seedling mortality in mostly neotropical tree species, and found that either distance- or density-dependent mortality occurred in most seedling populations, as predicted by Janzen and Connell.

Answers to many of these questions can only come from long-term observations of marked trees. In lowland dipterocarp forest in Malaysia one such long term study is the 2.02 ha plot established at Sungei Menyala in 1947 (Wyatt-Smith 1966), and was remeasured in 1981 by Manokaran & Kochummen (1987), making it one of the longest records, at 34 years, of tree growth and mortality in tropical forest. The plot included trees over 10 cm dbh, and contained a small strip (0.08 ha) in which saplings down to 1.3 m height were enumerated (Manokaran 1988). More recently, a 50 ha plot has been set up at Pasoh, Peninsular Malaysia, in lowland dipterocarp forest, in which all trees and lianes over 1 cm dbh have been enumerated (Kochummen *et al.* 1990, Manokaran & LaFrankie 1990). This plot is a companion to the 50 ha plot on Barro Colorado Island, Panama.

The most intense mortality often occurs in seedlings. The processes which

shape future species composition may therefore operate strongly on the seedling and sapling stage. The need for studies of the factors influencing seedling growth and mortality, and their rates in natural populations is often expressed (Richards 1952, Garwood 1983, Augspurger 1984a, Wyatt-Smith 1987, Hubbell & Foster 1990, Schupp 1990).

To date, studies of seedling ecology in tropical tree species have had a strong neotropical bias, and have generally considered one or a few species (Howe & Primack 1975, Sarukhàn 1978, Clark & Clark 1981, Augspurger 1983a, DeSteven & Putz 1984, Kitajima & Augspurger 1989). The fruiting pattern of dipterocarps is very different from that of the dominant trees in most neotropical forests. There mast fruiting is rare, and the dominant leguminous species often fruit annually or in alternate years (see above references). Few studies have looked at whole communities of seedlings in natural forest. Examples from the neotropics are the studies of Garwood (1982, 1983) on seedling establishment. At La Selva in Costa Rica, Li (1990) followed the fate of seedlings over six years. In total over 6400 seedlings in 194 species were censussed. In Australian rain forest, Connell *et al.* (1984) followed seedling growth over 18 years in tropical rain forest in Queensland, Australia, and tested two hypothesis relating to compensatory mechanisms. On the species level, they tested the prediction that common species have lower rates of survival and growth than rarer species. At the individual level, they tested the prediction that proximity to conspecific adults is deleterious for seedlings. In Sabah, Fox (1972) followed the fluctuations in dipterocarp seedling populations over 12 years. Liew & Wong (1973) compared mortality and growth of dipterocarp seedlings in virgin and logged forest in Sabah. Other studies of dipterocarp seedling ecology include those of Barnard (1956) and Becker (1983a). More recently, Turner (1990) reported on growth and survivorship in three species of *Shorea* in Penang, Malaysia, and Brown (1990) studied dipterocarp regeneration in artificial gaps in Danum Valley, Sabah.

One of the problems in undertaking a study at the scale of the community is often identification of the seedlings. The dipterocarps are well known, and although seedling leaves often differ from leaves of trees, dipterocarp seedlings in Sabah are generally easily recognised and identified.

1.2 DIPTEROCARP ECOLOGY

Emergent trees of Dipterocarpaceae dominate much of the rain forest of SE Asia. The family is centred in the Malesian rain forests, but ranges through the seasonal forests of the Indian sub-continent. In Asia, there are 12 genera with around 470 species. Borneo is the centre of diversity, with 287 species in 9 genera, 59% of which are endemic (Ashton 1982). Two genera, *Shorea* and *Hopea* are particularly species rich (Ashton 1988b).

Dipterocarps in non-seasonal forests are well-known for mast-fruiting, thought to have evolved to satiate seed predators (Janzen 1970). Fruiting occurs irregularly, but gregariously, usually 2-3 times per decade (Ashton 1982). Flowering can be highly synchronised: in Section *Mutica* (Light Red Merantis), sympatric species were found to flower in overlapping sequence at Pasoh, in Peninsular Malaysia (Chan & Appanah 1980), and trees could produce up to 4 million flowers (Appanah & Chan 1981). Heavy fruiting imposes stress on the trees, and diameter growth rates can be lower in years of mast-fruiting (Manokaran 1988). Ashton (1988a) has suggested that the fruit sepals have a photosynthetic function, in addition to dispersal. Despite the presence of elongated sepals, dispersal is often inefficient, leading to aggregated patterns of species distribution, with juveniles clustered around adult trees (Poore 1968, Ashton 1969). The one-seeded fruit have no dormancy, and the majority germinate within a few days of falling. Dipterocarps form ectomycorrhizal associations (Singh 1966, Becker 1983b), and limited spore dispersal has been suggested as an alternative reason for clumped spatial distributions (Ashton 1982).

Seeds germinate in the shade. Mortality can be very high immediately after germination, resulting in large fluctuations in numbers over time (Fox 1972, Whitmore 1984). Growth rates in closed forest are very low (Fox 1972), but seedlings can persist for many years (Fox 1972, Wyatt-Smith 1958), forming 'seedling banks' (Meijer & Woods 1964, Harper 1977). Species differ in their tolerance to periods of suppression (Fox 1972): Wyatt-Smith (1958) suggested that *Shorea leprosula* and *S. parvifolia* required a gap within ten years to commence growth. Nicholson (1960) found that five species, including *S. leprosula* and *S. johorensis* required shade for establishment, and could respond to full light after 18 months. Nicholson (1960), Sasaki & Mori (1981) and Brown (1990) showed that species differed in their responses to light. Responses to increased light following canopy opening are especially strong in the

light hardwood Red Meranti species and *Parashorea* (Nicholson 1965b, Liew and Wong 1973, Whitmore 1984), though sudden exposure to high irradiance can cause damage or even death (Whitmore 1984).

Dipterocarps have been divided by foresters, on the basis of field experience and wood density, into two groups, the light hardwoods: light demanding, fast growing species, and heavy hardwoods: slow-growing, shade tolerant species (Meijer & Wood 1964, Burgess 1966, Wyatt-Smith 1966), though there is likely to be a continuum of responses (Whitmore 1984). The two groups are assumed to have differing requirements for regeneration: shade tolerant species reputedly respond to smaller gaps with increased growth (release), while in the light-demanding species, a larger gap is required for release.

From a survey of virgin forest near Sandakan, Sabah, Nicholson (1965b) concluded that growth of dipterocarps from large sapling size to the canopy was fast, resulting in low numbers of small trees in the understorey, especially in fast-growing species (Fox 1967). This is a characteristic feature of the size class distributions of light-demanding dipterocarps (Whitmore 1984). The presence of large numbers of seedlings of commercially desirable species of dipterocarps, and the shortage of small trees is the basis of the Malayan Uniform System of silviculture, under which clear-felling every 50-70 years is followed by regeneration from the established seedlings. Wong (1973) studied growth in 10-year old regenerating forest at Segaliud-Lokan, Sabah, and estimated that some species could attain 8 ft girth (≈243 cm gbh, 80 cm dbh) in 60 years.

1.3 AIMS

The aims of this study were:

- to describe the dipterocarp seedling population on a relatively large scale (two hectares);
- to measure growth and mortality rates of large populations of dipterocarp seedlings under natural conditions, and to compare rates between species;
- to describe the spatial patterns of dipterocarp seedlings by fully mapping all individuals;

- to relate seedling distribution patterns to the positions of adult trees.
- to evaluate the Escape Hypothesis and Compensatory Mechanisms Hypothesis of Janzen (1970), Connell (1971, 1978), Howe & Smallwood (1982) and Connell *et al.* (1984).

The chart in Figure 1.1 shows how data from the seedling enumerations, supported by data from the tree enumerations, were used to answer questions on different aspects of these hypotheses.

1.4 THE STUDY SITE

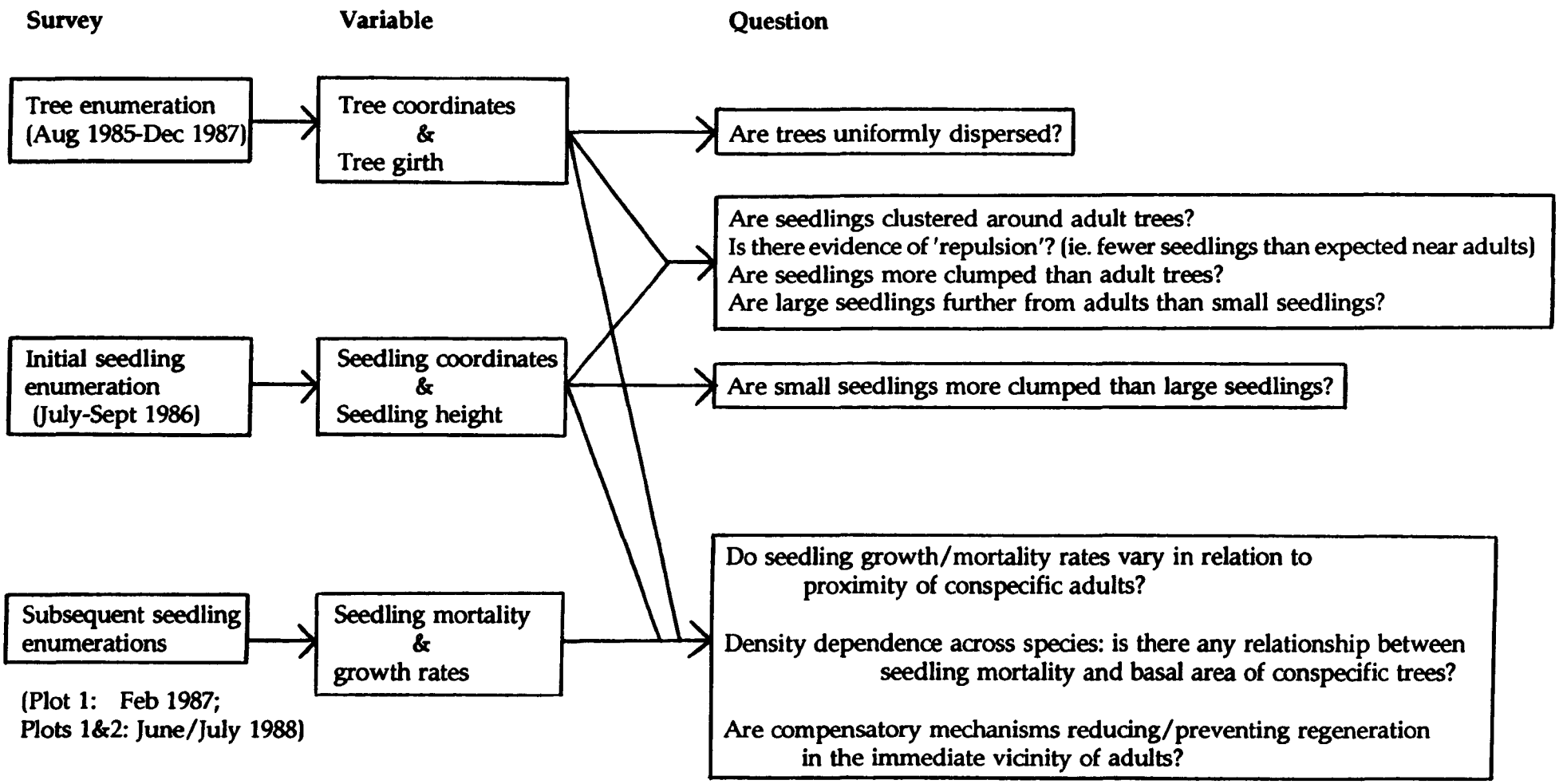
1.4.1 Location

This study was carried out in the Danum Valley Conservation Area, Sabah, Malaysia (4°58'N, 117°48'E), a 438 km^2 area of lowland dipterocarp rain forest retained for conservation purposes by Yayasan Sabah and the Sabah Forest Department. The area lies by the Segama River, around 70 km inland from Lahad Datu (Figure 1.2).

1.4.2 Climate

Rainfall records at the Danum Valley Field Centre (DVFC) began in mid-1985, and annual rainfall up to the end of 1990 averaged 2822 mm (Marsh & Greer 1992). The area lies to the south of the main monsoon belt, but is affected by it. Strong squally winds are therefore rare, but there are seasonal trends in rainfall, with drier periods in April/May and in September between monsoons. The northeast monsoon brings higher rainfall between November and March. Mean annual temperature is 26.7°C, with mean maximum and minimum of 30.9°C and 22.5°C (Walsh 1990). Within the forest, mean maximum and mean minimum temperatures were 28.4°C and 21.2°C (Brown 1990). Annual mean relative humidity (recorded in the DVFC clearing) was 94.5%, falling to 72% at 1400 hrs (Walsh 1990).

Figure 1.1 Summary of variables and their roles in investigating aspects of the Escape and Compensatory Mechanisms Hypotheses.



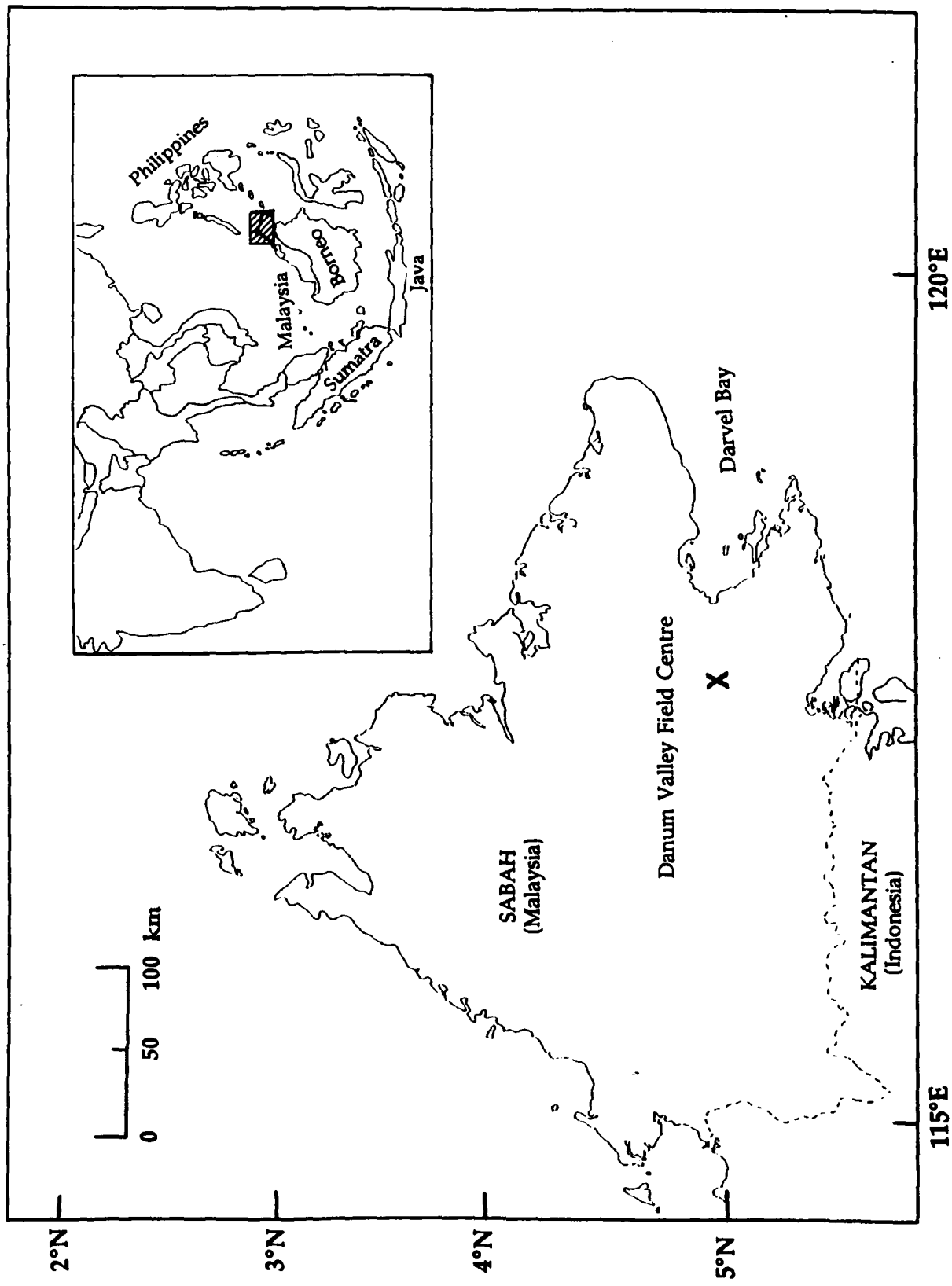


Figure 1.2 Map showing the location of the Danum Valley Field Centre, in Sabah, East Malaysia.

1.4.3 Topography and soils

The topography in the study area is undulating, with occasional steep-sided gullies. The soils in the vicinity of the DVFC are classified as orthic acrisols in the Bang Association, developed over Tertiary sandstones, mudstones and shales of the Kuamut Formation (Wright 1975).

1.4.4 Vegetation

The forest around the study area is dominated by emergent trees of Red Meranti species, especially *Shorea johorensis, S. parvifolia and S. argentifolia,* together with *P. malaanonan*. *Koompassia excelsa* (Leguminosae) is a notable emergent tree in the area. The forest is classified as Type A (*Parashorea malaanonan* forest) in Fox's (1972) classification of Sabah forest types. This is the dominant forest type on coastal areas in north-east and east Sabah and in the upper Segama catchment, and is characteristic of more fertile soils and areas of lower rainfall (Fox 1972). *Shorea guiso*, usually present (Fox 1972), appears to be rare around the study area.

1.5 BACKGROUND AND FIELD METHODS

1.5.1 Background

The study was carried out in the two 4 ha plots established by D. M. Newbery, University of Stirling (Newbery *et al.* 1992) in 1985-86. The seedling enumeration was started while I was employed to carry out enumeration of the trees in the University of Stirling plots. Tree enumeration and identification methods are detailed in Newbery *et al.* (1992). The plots provided replicate areas in which every tree (≥10 cm gbh, ca. 3.2 cm dbh) has been mapped, tagged, measured and identified as part of the project, and I was able to draw on the project data-set and use data on the dipterocarp trees to supplement the seedling study.

The two 4 ha plots had been established on broad ridges 200 m apart. The plots were 400 x 100 m with the long axes aligned north-south, parallel to the ridge direction, 500 m west of the River Segama, and at 70 m elevation from the river. The plot areas were chosen to be as similar in topography as possible and representative of the forest structure in the eastern part of the Danum Valley Conservation Area. The plots are now designated areas for long term research, under the protection of Sabah Forest Department and Yayasan Sabah.

Trees in Plot 1 were enumerated between mid-September 1985 and mid-March 1986, and Plot 2 trees, from mid-November to mid-December 1986. Phase 1 of taxonomic identification was carried out during the initial enumeration by E. Campbell. In July 1988, the identifications of most of the large trees (ca. 80 cm gbh and larger) in both plots were checked in the field by Sabah Forest Department (SFD) personnel. In addition, I checked the identifications of all the smaller dipterocarps in both plots. The taxonomy of all trees was subsequently reviewed and revised (Phase 2) by Lee Ying Fah of SFD and C. Ridsdale of the Rijkherbarium, Leiden, in a complete check of all surviving trees in 1989. The dipterocarp trees were thus checked three times and named on the basis of field characters and herbarium specimens. Infertile specimens of each dipterocarp species, including samples of juvenile material, are included in the reference collection of vouchers deposited at the Rijksherbarium, Leiden. Fertile material of one species, *Vatica sarawakensis* is held at RBG, Edinburgh.

In July 1988, most dipterocarp trees in Plot 1 were re-measured (limitation of time meant that large buttressed trees could not be re-measured) and all dipterocarp trees in Plot 2 were revisited and mortality recorded.

1.5.2 Seedling enumeration methods

Dipterocarp seedlings were enumerated in a 2 ha area of Plot 1. The southern 2 ha block was chosen because dipterocarp seedling regeneration had been observed during the tree enumeration work, and the steeper areas in the northern half of the plot were avoided. From familiarity with the plot, a 2 ha area was judged to contain sufficient numbers of seedlings to allow comparisons between different species and size classes. The area was also large enough to analyse the large-scale spatial patterns

of seedlings, and in particular, to attempt to relate these to the positions of adult trees. In Plot 2, the area chosen was in the southern end, where the topography was similar - both areas lay at the lower ends of ridges where the slopes were gentle. Species composition of canopy and emergent dipterocarps was similar to that in the seedling survey area of Plot 1 (mainly Red Merantis: *S. johorensis, S. parvifolia, S. argentifolia*; and *Parashorea malaanonan*). Because of time constraints, a smaller area was surveyed, a central block of 60x80 m (0.48 ha). The topography of the seedling study areas and their locations within the main enumeration plots are illustrated in Appendix 1.

In the study, a seedling was defined as any individual less than 10 cm gbh, the minimum girth for inclusion in the tree enumeration. Each dipterocarp seedling was identified and mapped to the nearest 0.1 m with reference to the previously mapped trees. Plot co-ordinates were later assigned to each seedling with reference to the south-west corner of each plot (ie. on the same co-ordinate system as the tree data-set). Seedlings were tagged with a yellow plastic tag, numbered with indelible (and fadeproof) pen, and loosely looped around the stem at least 10 cm below the apex. This avoided damaging the shoot tip, and delayed the tag dropping to ground level and becoming buried in litter as the lower branches were shed. Seedlings were identified in the field from leaf characters, and with reference to the identifications of the enumerated trees; although adult and juvenile leaves of dipterocarps can be quite different, leaf characteristics of seedlings are similar to those of small trees of the same species in the understorey. Height was measured as the vertical distance from ground level to the base of the highest living apical bud. If the apical bud was dead, height was measured to the highest living point. Seedlings less than ca. 2.5 m tall were measured with a steel tape measure. Taller seedlings were measured with a telescopic measuring pole, allowing seedlings up to around 6 m tall to be measured accurately without bending the stem. Above about 6 m it became difficult to measure height accurately, especially if surrounding vegetation was dense, so 6 m was chosen as the upper limit for height measurement. Taller seedlings were assigned to a single category, >6 m. Also recorded were: girth of seedlings ≥300 cm tall; condition of the highest apex, whether dead or missing; and presence of stem damage, whether seedling stem showed scars of previous stem breakage (ie. if the stem showed a marked discontinuity in size or a pronounced kink along its length [Putz & Brokaw 1989]).

Seedlings in Plot 1 were enumerated between mid-July and mid-September 1986, and Plot 2, September to October 1986. Date of measurement was recorded to the nearest week. In early February 1987, Plot 1 seedlings were revisited. If there was no sign of a seedling or tag after a search of the vicinity, the seedling was recorded as dead. Living seedlings were remeasured, and condition variables re-recorded. Seedling deaths judged to be caused by falling debris were noted. Individuals missed in the first survey were tagged, mapped and measured. Seedlings in Plot 2 were revisited but not remeasured, and missed seedlings included. The third enumeration was in June-July 1988, when all seedlings in both plots were located if still alive, and remeasured and surveyed as above. Further seedlings, missed in previous enumerations, were tagged, mapped and measured.

For seedlings that had died, category of death was recorded where possible as:

- "standing dead": stem still standing but clearly dead
- "no trace": no sign of seedling after searching the vicinity
- "litter-fall": dead seedling visible covered by fallen debris, or debris completely covering position of seedling.

During the second enumeration, *V. dulitensis* seedlings less than 20 cm tall (the 1985 cohort) were not remeasured, but mortality was recorded. Height of all larger seedlings was measured. The 1985 cohort was distinguished in the field by size (less than 20 cm height) and number of leaves (one or two). Growth and mortality rates for this cohort were calculated and analysed separately from older seedlings in the species.

During the period August 1985 to May 1988, no dipterocarp flowering was recorded in the immediate area, except for *Vatica dulitensis* in Plot 1 which fruited heavily in August-September 1985 and produced a large number of seedlings. In June and July 1988 there was limited flowering of a few *Shorea* spp, *Parashorea* and *Vatica sarawakensis* in the vicinity of Plot 1, but subsequent fruit were not viable (N. Brown, *pers. comm.*), and germinating seeds of *Vatica umbonata* were found 1 km west of Plot 1 in July 1988. Individuals first recorded during the second or third enumerations were therefore assumed to have been present from the first census, on the basis of their large size, and because no dipterocarp fruiting was observed in the study areas during the entire study. Such individuals were included in analyses of spatial pattern, but were excluded from estimates of growth and mortality if they were not

measured at the start of the interval.

A summary of the variables measured and how these were used to evaluate aspects of the Escape and Compensatory Mechanisms Hypotheses is given in Figure 1.1.

1.5.3 Data analysis

The data were stored and analysed on the University of Stirling VAX/VMS and HP mainframe computers, using a combination of specially written FORTRAN programmes, routines from the NAG library (NAG 1980), and the SPSS^X (SPSS^X Inc. 1983) and MINITAB (Ryan *et al.* 1985) statistical packages.

P values in tables and figures throughout are: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

1.6 THE PLOTS

1.6.1 Composition and structure

The family composition and structure of the plots are described in detail in Newbery *et al.* (1992). Total basal area of trees over 10 cm gbh was 30.7 m^2ha^{-1} (mean of both plots) and 26.6 m^2ha^{-1} for trees over 30 cm gbh. The plots were dominated by dipterocarps, which contributed on average almost half the basal area and 16% of the density. Girth distributions of the dipterocarp trees show a linear relationship between the logarithms of gbh and frequency, indicating a stable size distribution and suggesting no recent disturbance (Newbery *et al.* 1992).

1.6.2 The dipterocarp species

The species of dipterocarps present in the seedling study areas of the main plots cover a wide range of ecological types (canopy and emergent species, light and

heavy hardwoods) and taxonomic similarities and differences. There is a trio of closely related species of Light Red Merantis (LRM, Section *Mutica*): *Shorea argentifolia*, *S. leprosula* and *S. parvifolia*. They are large emergent trees, with strongly light-demanding, fast-growing saplings (Meijer & Wood 1964, Fox 1972, Ashton 1982, Whitmore 1984). *S. johorensis* (Red Meranti, Section *Brachypterae*) is one of the dominant species in the area, also a large emergent with light-demanding sapling, but generally with heavier wood than the preceding species. This species forms a 'seedling bank' of suppressed small seedlings (Meijer & Wood 1964). Two Dark Red Merantis (Sect *Brachypterae*) occur: *S. pauciflora* is a dominant emergent species, producing heavy hardwood timber, and growing to very large size. The largest tree in the plots was of this species (554 cm gbh). *S. fallax* is smaller, but still emergent. The remaining *Shorea* species, *S. agamii*, is a White Meranti, Section *Anthoshorea*, and forms a large tree (Ashton 1982). The other major emergent tree in the area, *Parashorea malaanonan* is classified as light hardwood (Burgess 1966) and generally has abundant suppressed seedlings (Meijer & Wood 1964). Three canopy species were present, all shade tolerant, and classified as medium to heavy hardwood (Burgess 1966): *Hopea nervosa*, *Vatica dulitensis* and *V. sarawakensis*.

1.7 OVERVIEW OF CONTENTS

The following seven chapters cover two main themes. The first part considers the dynamics of the dipterocarp seedling populations, while the second part explores the spatial distribution patterns.

The seedling populations are described in Chapter 2. Seedling mortality and growth rates are examined in Chapters 3 and 4 respectively. Chapter 5 considers the relationships between seedling growth and mortality rates, on an individual and species basis. Growth and mortality rates of trees (≥10 cm gbh) are briefly described in Chapter 6, and compared with the rates in seedlings.

In Chapter 7, seedling spatial patterns are explored and compared using a variety of tests. Patterns of trees are briefly described and compared with seedling patterns. In Chapter 8, the relative dispersion patterns of seedlings and trees are described, and the implications for recruitment considered.

CHAPTER 2

THE SEEDLING POPULATIONS

2.1 SPECIES COMPOSITION OF SEEDLINGS

In total, 14 dipterocarp species were present as seedlings in both seedling study areas (Table 2.1). The study area in Plot 1 (2.0 ha) contained 13 species and Plot 2 (0.48 ha) ten, with nine species common to both. A list of all dipterocarp species recorded in the two main enumeration 4 ha plots (trees over 10 cm gbh) is provided in Appendix 2. Taxonomic groupings and authorities are given.

Seedlings of the Red Meranti, *Shorea johorensis*, and three Light Red Merantis (LRM), *S. argentifolia*, *S. leprosula* and *S. parvifolia*, were present in the seedling study areas of both plots, as was *S. fallax*, a Dark Red Meranti (DRM). Other species common to both study areas were *Parashorea malaanonan*, *Hopea nervosa*, *S.* cf. *symingtonii* and *Vatica sarawakensis*. *S. pauciflora* and *S. agamii* seedlings and trees were recorded in Plot 1, but they were both completely absent from Plot 2, as trees or seedlings. *S. agamii* occurred as well-scattered seedlings, and a single adult tree in Plot 1. *S. pauciflora* was one of the dominant emergent trees in Plot 1, along with *S. johorensis* and *S. argentifolia*, and seedlings were abundant. *S. pilosa*, present in the study area of Plot 2, was absent from the study area of Plot 1, but a single cluster of trees and seedlings was recorded in the plot some 100 m from the seedling study area. The most abundant species, *V. dulitensis* in Plot 1, occurred as a dense patch of seedlings clustered around a single adult tree. Almost half of these seedlings had appeared between August and October 1985. This species was absent from the study area of Plot 2, but both trees and seedlings were frequent in other areas of the plot. Maps illustrating the spatial distributions of seedlings and adult trees are given in Appendix 3.

Table 2.1 Numbers, densities (ha^{-1}) and percent contribution of different species of dipterocarp seedlings, and of Light Red Merantis (LRM) and Dark Red Merantis (DRM), recorded in the study areas of Plot 1 and Plot 2 (2.0 ha and 0.48 ha respectively). Presence as adults (≥80 cm gbh in *Vatica* spp. and *H. nervosa*; ≥100 cm gbh in other species) within the seedling study areas (++) and the remaining areas of the 4 ha plots (+) is indicated.

	Number		Density (ha^{-1})			% contribution			Presence of trees	
Species ♦	Plot 1	Plot 2	Plot 1	Plot 2	mean	Plot 1 *	Plot 2	mean *	Plot 1	Plot 2
S joho	333	134	166.5	279.2	188.3	9.1	11.2	9.7	++	++
S arge	245	43	122.5	89.6	116.1	6.7	3.6	5.9	++	++
S lepr	157	18	78.5	37.5	70.6	4.3	1.5	3.6	++	++
S parv	210	112	105.0	233.3	129.8	5.8	9.3	6.6	++	++
S fall	624	106	312.0	220.8	294.4	17.1	8.8	15.1	++	++
S pauc	554	0	277.0	0.0	223.4	15.2	-	11.4	++	
P mala	589	280	294.5	583.3	350.4	16.1	23.4	17.9	++	++
H nerv	138	391#	69.0	814.7#	213.3#	3.8	32.6	10.9	++	++
S agam	161	0	80.5	0.0	64.9	4.4	-	3.3	++	
S sp10	19	0	9.5	0.0	7.7	0.5	-	0.4		
S symi	7	8	3.5	16.7	6.0	0.2	0.7	0.3		
S pilo	0	24	0.0	50.0	9.7	-	2.0	0.5	+	++
V dul1↕	515	0	257.5	0.0	207.7	14.1	-	10.6	++	+
V dul2↕	336	0	168.0	0.0	135.5	-	-	-	++	+
V sara	97	82	48.5	170.8	72.2	2.7	6.8	3.7	++	++
LRM	612	173	306.0	360.4	316.5	16.8	14.4	16.2		
LRM+S joho	945	307	472.5	639.6	504.8	25.9	25.5	25.8		
DRM	1178	106	589.0	220.8	517.7	32.2	8.8	26.5		
Shorea spp.	2310	445	1155.0	927.1	1110.9	63.3	37.1	56.8		
Total	3649* 3985	1198#	1824.5* 1992.5	2495.7	1908.5* 2089.9	100.0	100.0	100.0		

♦ see Appendix 2 for abbreviated names

* excluding *V. dulitensis* 1985 cohort (V dul2)

\# incomplete survey of *H. nervosa* (0.34 ha); values for density and % contribution adjusted for estimated density

↕ V dul1 - seedlings older than 1985 cohort
V dul2 - seedlings of 1985 cohort

2.2 SEEDLING NUMBERS AND DENSITIES

Seedling numbers and densities (ha^{-1}) of individual species and species groups are given in Table 2.1. Densities of total dipterocarp seedlings were quite similar in the two plots, if *V. dulitensis* is included, at about 2000 seedlings ha^{-1}. 1992 ha^{-1} were in Plot 1 and 2496 ha^{-1} in Plot 2. The mean was 2090 ha^{-1}. If *V. dulitensis* is excluded, the Plot 1 total would be reduced to 1567 ha^{-1}, and the overall mean for the two study areas would be 1747 ha^{-1}.

Densities of *Shorea* species seedlings were similar in the two study areas, with 1115 ha^{-1} in Plot 1 and 927 ha^{-1} in Plot 2. Overall mean density of all *Shorea* species was 1111 ha^{-1}. Both plots also had similar densities of Light Red Merantis, 306 ha^{-1} and 360 ha^{-1} in plots 1 and 2 respectively (overall mean 316 ha^{-1}). *S. johorensis* was more abundant in Plot 2. Plot 1 was much richer in Dark Red Merantis (589 ha^{-1} compared to 221 ha^{-1}), due to the presence of *S. pauciflora* (absent from Plot 2) and the greater abundance of *S. fallax*. The three remaining species occurring in both plots, *P. malaanonan*, *H. nervosa* and *V. sarawakensis*, were all more abundant in Plot 2. Densities of different species in the two plots were not significantly rank correlated (Spearman r_s=0.417, n=9, P>0.05). The species which differed most in rank (including only species common to both plots) were the most abundant species in either plot: *H. nervosa*, the most abundant in Plot 2, was ranked seventh in Plot 1, while the most abundant in Plot 1, *S. fallax*, was ranked fifth in Plot 2. There were similarities, however. *P. malanonaan* and *S. johorensis* were ranked second and third respectively in both plots (of the species common to both plots), and *S.* cf *symingtonii* was the least abundant species in both plots.

Overall mean densities of total Red and LRMs, and total DRMs were virtually identical, with values of 518 ha^{-1} for DRMs and 505 ha^{-1} for Red and LRMs, forming 26.5% and 25.8% respectively of total dipterocarp seedling density. *Shorea* species together contributed 57% of total mean density, rising to 65% if *V. dulitensis* is excluded. The single most abundant species overall was *P. malaanonan*, contributing 17.9% to total density, with a mean density of 350 ha^{-1}. *V. dulitensis* was next most abundant (1985 cohort and older seedlings combined), contributing 16.4%, followed by *S. fallax* with 15%.

Curves of log density versus rank abundance for the two study areas are shown in Figure 2.1. In both plots, the decrease in log density with increasing rank

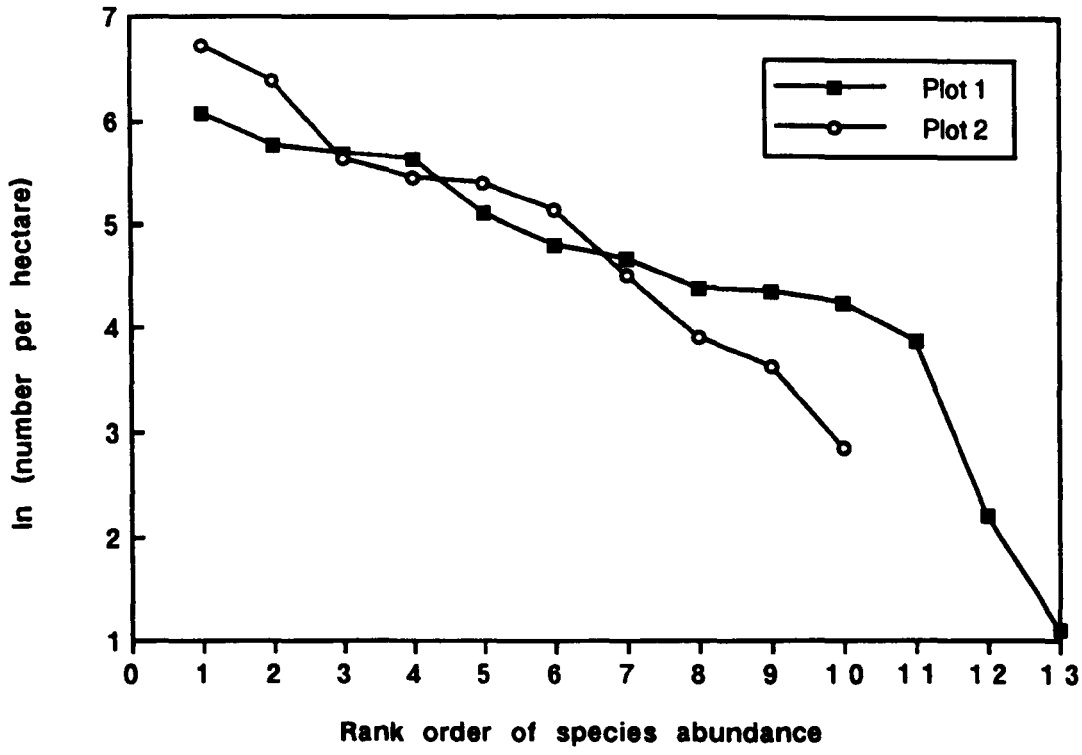


Figure 2.1 Seedling density (numbers per hectare) in each species plotted against its rank abundance in Plots 1 and 2.

is approximately linear. The curve for species in Plot 2 is initially steeper, while the Plot 1 curve drops sharply to the two least abundant species. The range of values in both plots is similar, though the most abundant species in Plot 2 occur at higher density, and form a higher proportion of total density, than in Plot 1. The two most abundant species in Plot 2 make up 33% and 23% of total density, compared with 21% and 17% in Plot 1 (Table 2.1). The least abundant species in Plot 1, with less than 10 individuals per hectare, are at lower density than the least abundant in Plot 2.

2.3 HEIGHT FREQUENCY DISTRIBUTIONS

2.3.1 Variation between plots

Histograms of height class frequencies (measurements from the first and final enumeration) of all species pooled are shown in Figure 2.2. Height distributions were significantly different between the two plots (χ^2=133.06, d.f.=13, P<.001). There was a greater proportion of small seedlings in Plot 2 (Section 2.3.4). Modal height class in Plot 2 was 26-50 cm, and included 26% of the population, whereas in Plot 1, 51-75 cm was the modal class (if *V. dulitensis* is excluded), containing 18% of the population (Figure 2.2).

2.3.2 Variation between species

Histograms of height class frequencies (measurements from the first enumeration) for separate species are illustrated in Figure 2.3. For most species in Plot 1, modal height lay in the three classes from 26 cm to 100 cm. The exceptions were *V. dulitensis* with a very strong peak in the smallest size class: 83% were less than 25 cm tall, and *V. sarawakensis*, in which modal height class was 126-150 cm (Figure 2.3). Several species had small peaks in the 201 cm to 250 cm classes. Secondary peaks were marked in *H. nervosa* and *V. sarawakensis*, both of which had irregularly shaped height frequency histograms. In contrast, in Plot 2, modal height class in most species was 26 - 50 cm. Only two species, *V. sarawakensis* and *S. johorensis* had modal frequency in a taller size class (51 to 75 cm in both species). *P.*

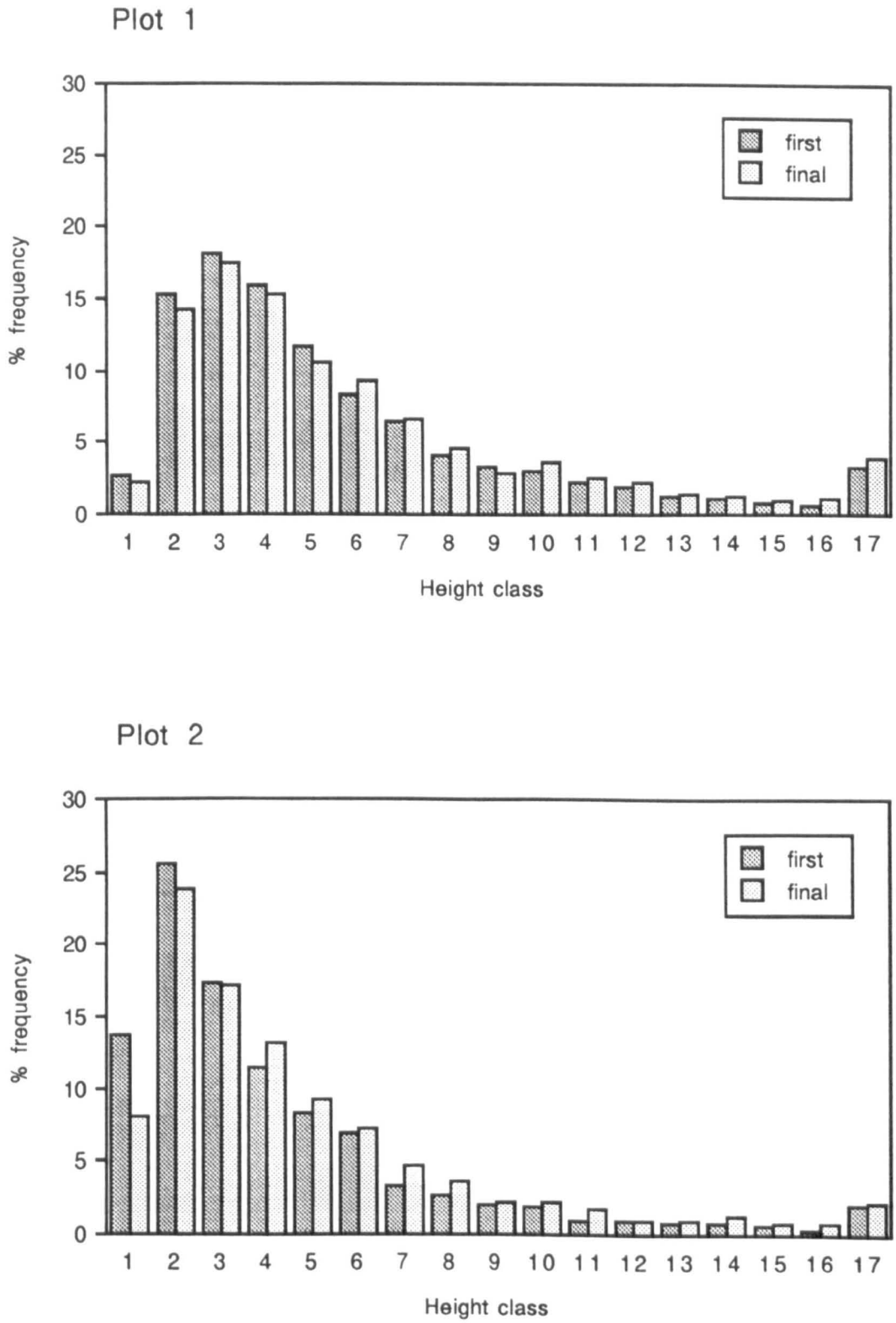


Figure 2.2 Frequency distributions of seedling heights at the first and final enumerations (July-Sept. 1986 and Feb. 1988 respectively) for all individuals pooled in Plots 1 and 2 (excluding *Vatica dulitensis* in Plot 1). Height classes 1 to 16 are in 25 cm intervals; class 17, >400 cm.

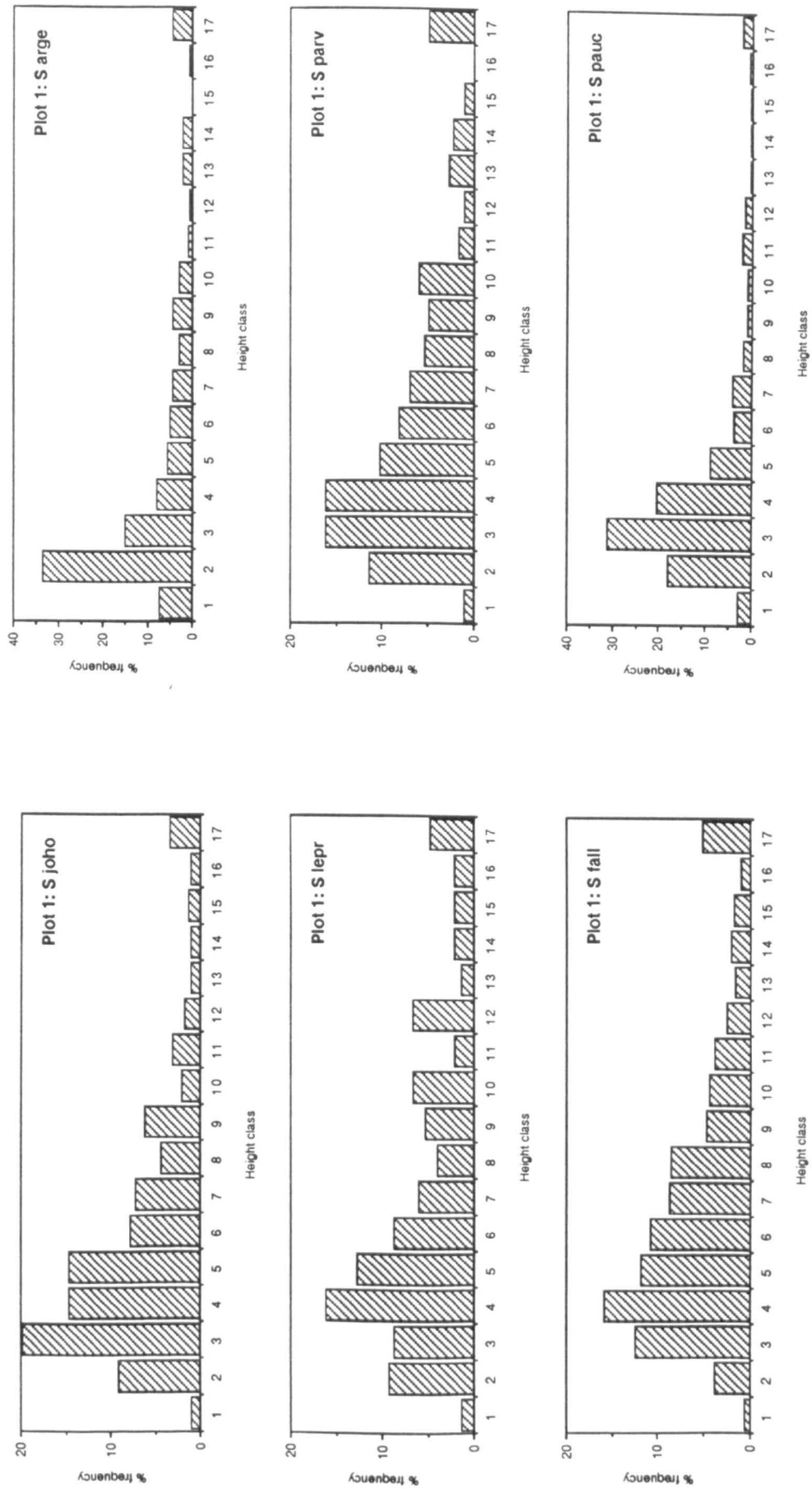


Figure 2.3 Frequency distributions of heights at the first enumeration for different species in Plots 1 and 2. Height classes 1 to 16 are in 25 cm intervals; class 17, >400 cm.

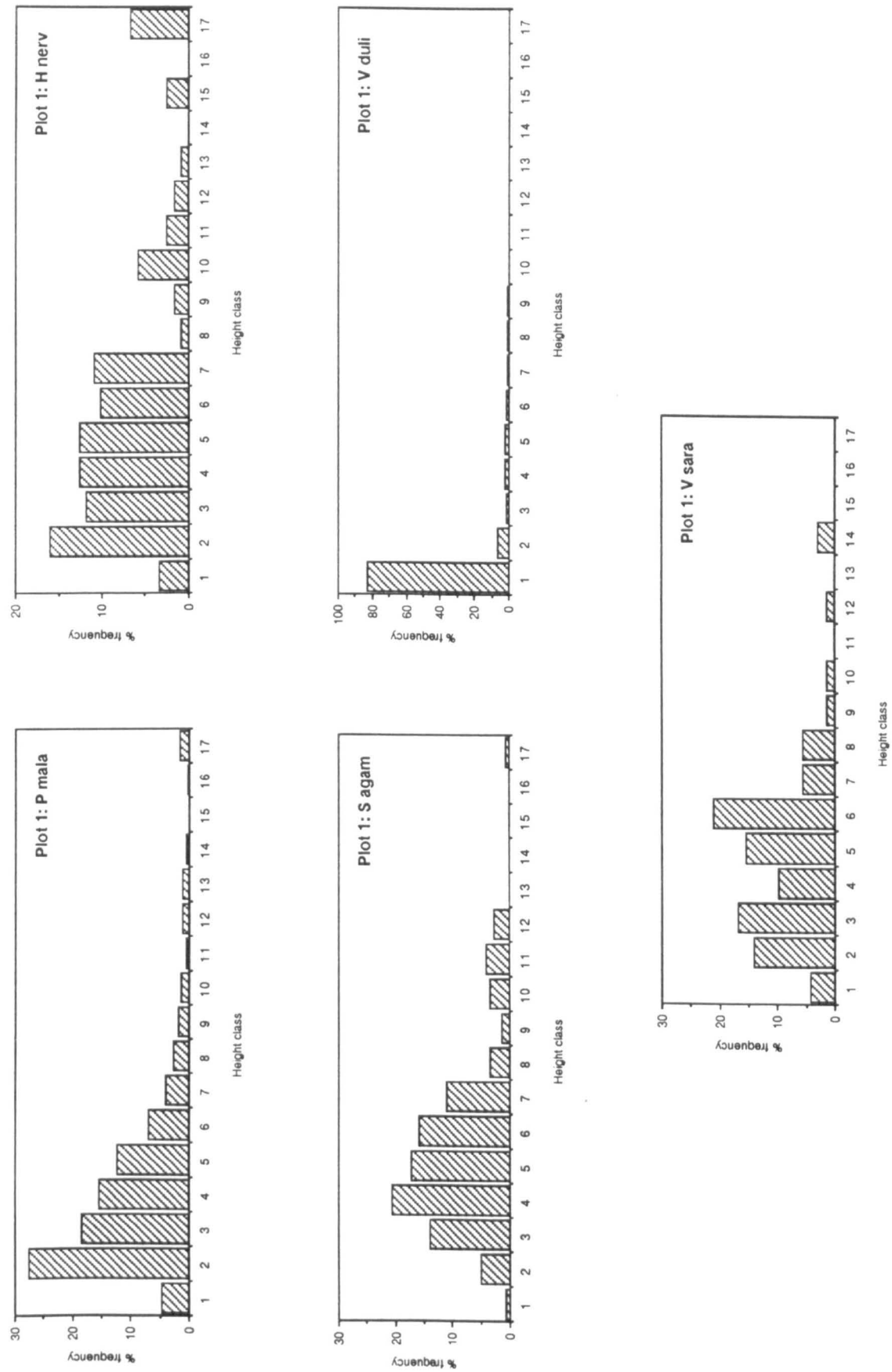


Figure 2.3 (continued) Frequency distributions of heights at the first enumeration for different species in Plots 1 and 2. Height classes 1 to 16 are in 25 cm intervals; class 17, >400 cm.

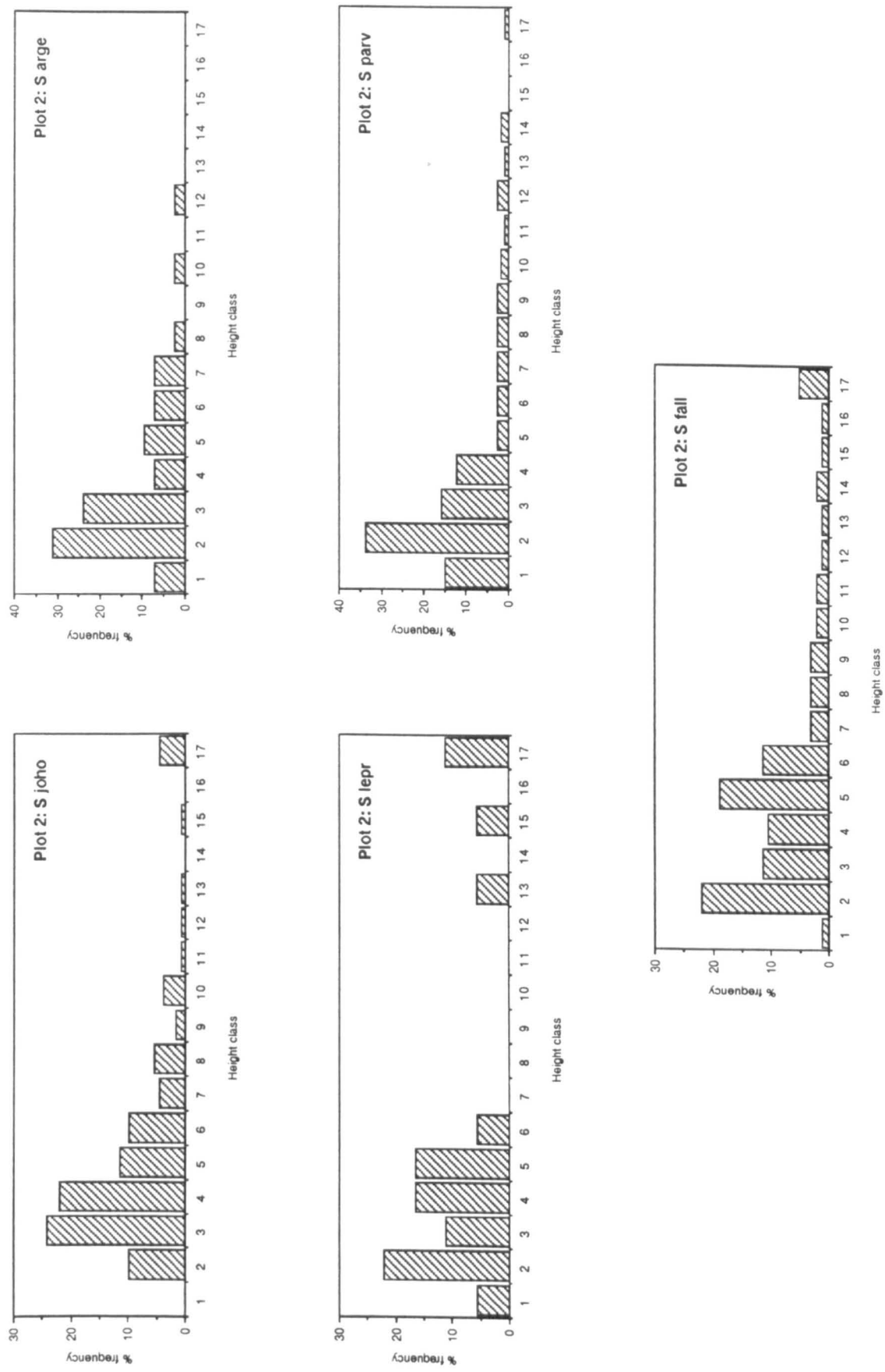


Figure 2.3 (continued) Frequency distributions of heights at the first enumeration for different species in Plots 1 and 2. Height classes 1 to 16 are in 25 cm intervals; class 17, >400 cm.

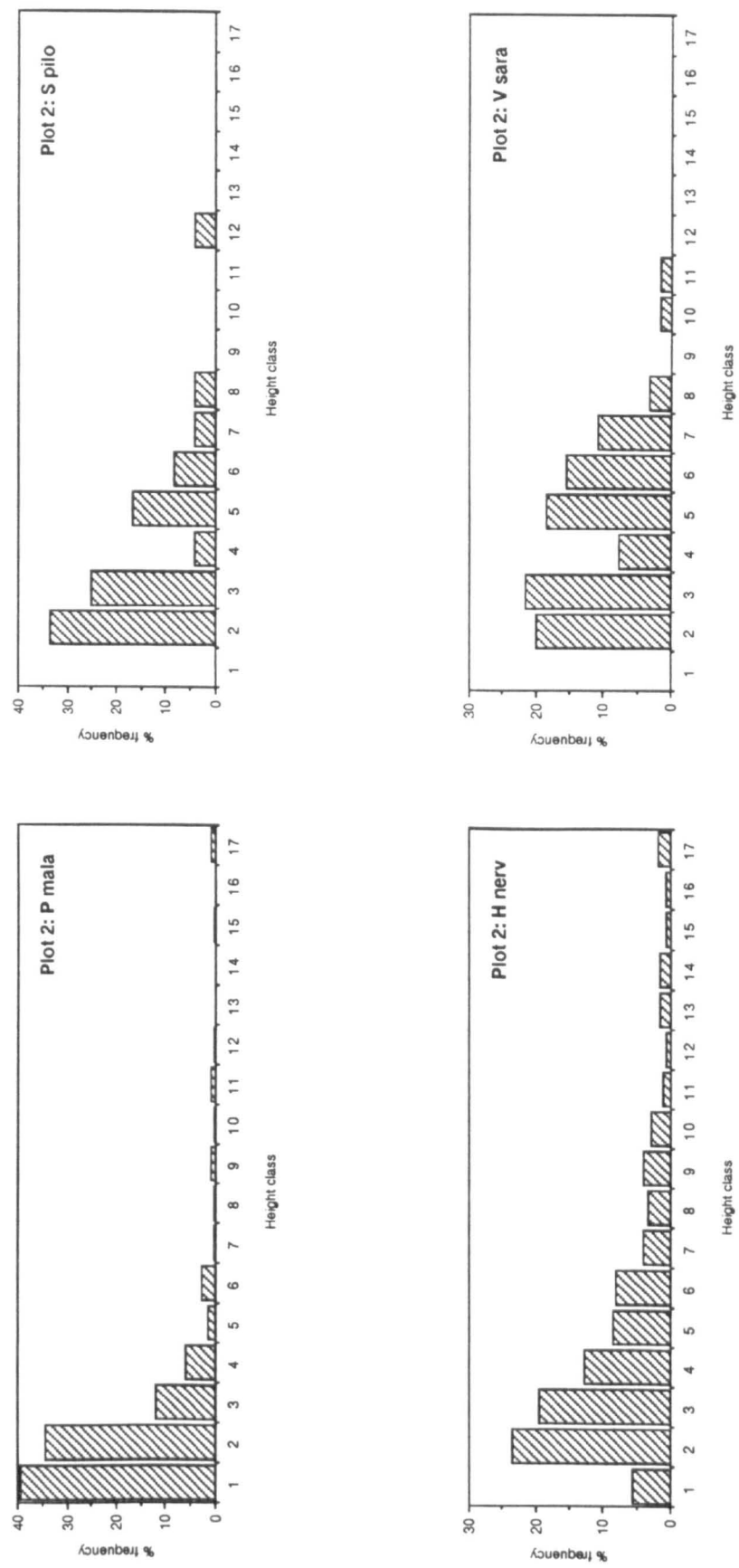


Figure 2.3 (continued) Frequency distributions of heights at the first enumeration for different species in Plots 1 and 2. Height classes 1 to 16 are in 25 cm intervals; class 17, >400 cm.

malaanonan differed from all other species (except *V. dulitensis*) in having the greatest frequency in the smallest height class: 39% were less than 25 cm tall. As in Plot 1, the height frequency histogram of *V. sarawakensis* had multiple peaks, at 51-75 cm, 101-125 cm and 226-275 cm, corresponding closely to the peaks in Plot 1. The histogram for *S. fallax* also included two marked peaks, the peak at 26-50 cm representing the patch of small seedlings below a single dead emergent adult, identified as *S. fallax* from bark characters. *S. johorensis* and *S. argentifolia* had similar height distributions in the two plots, but *S. parvifolia* differed more: the distribution in Plot 2 was more leptokurtic, and peaked in a smaller height class.

Height frequency distributions (using height at first enumeration) were compared within species between the two plots with a Kolmogorov-Smirnov test. Significant differences ($P<0.05$) existed in four species: *S. parvifolia*, *S. fallax*, *P. malaanonan* and *H. nervosa*. In all four species, median height was lower in Plot 2.

2.3.3 Frequency of small and large seedlings

Differences between species in the proportion of small seedlings in the population may indicate differences in the ability of the seedlings to tolerate low light levels and remain suppressed, maintaining a 'seedling-bank' (Harper 1977) of small (≤30 cm tall) seedlings awaiting gap creation. This has been recorded in *S. johorensis* and *P. malaanonan* (Meijer & Wood 1964). Fruiting of dipterocarps (with the exception of *V. dulitensis*) had not been recorded in the area for at least three years prior to the start of this study (July 1986), so it was assumed that even the smallest seedlings recorded had survived at least three years.

The largest saplings present in the population have either succeeded in growing in the low light levels of the understorey, or have grown rapidly in response to canopy opening. In either case, they are likely to be at a competitive advantage to smaller saplings (Caldwell 1987). Also, survival rates in large saplings were generally higher than those of small seedlings (see Chapter 3.4). These individuals can therefore be thought of as the most likely to succeed. Differences between species in the proportions of small seedlings (≤50 cm) and large saplings (>250 cm) are illustrated in Figure 2.4.

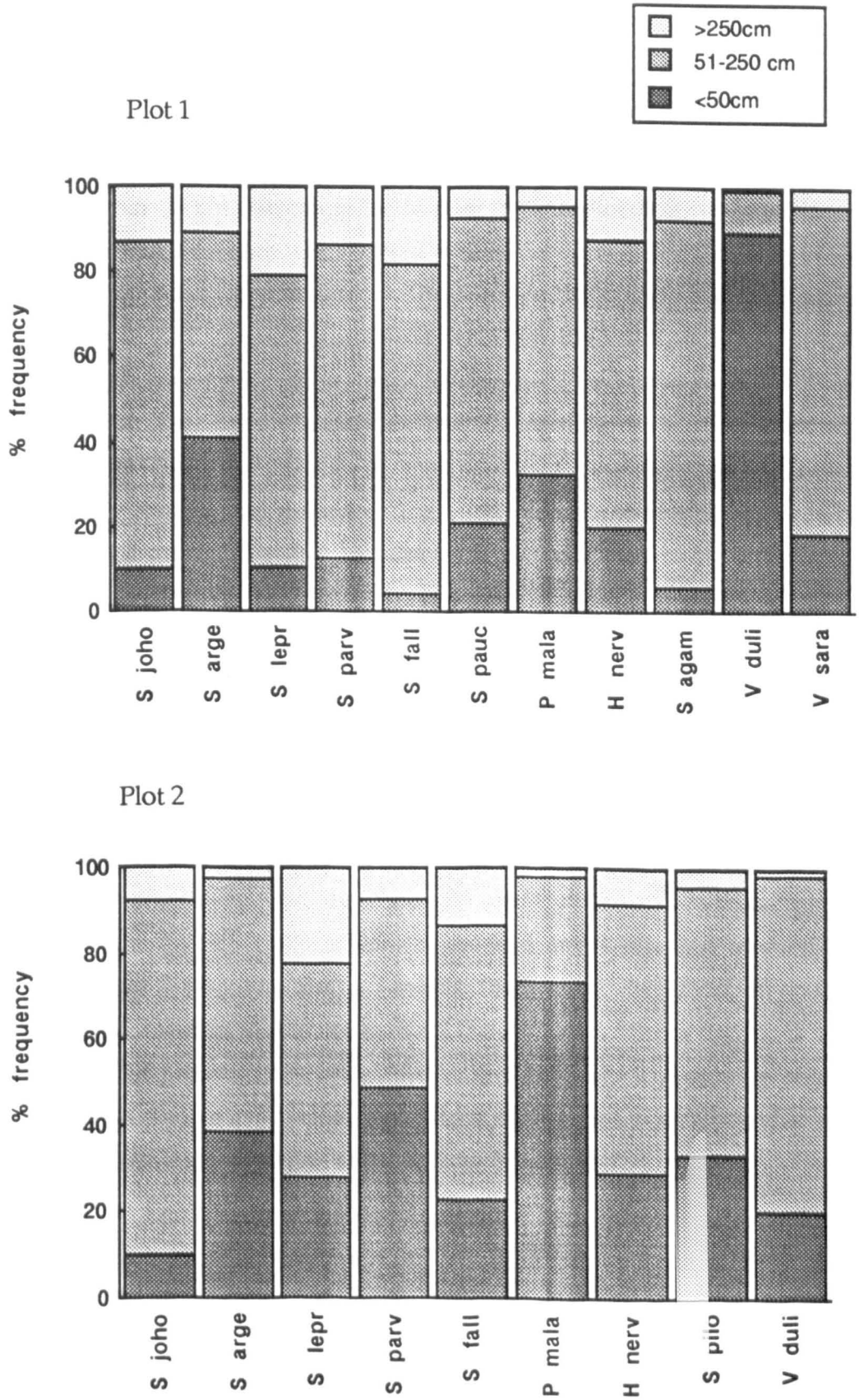


Figure 2.4 Percentage of small (≤50 cm), medium (51-250 cm) and large (>250 cm) seedlings in different species in Plots 1 and 2 (data from first enumeration).

2.3.3.1 Small seedlings

The proportion of small seedlings was greater in Plot 2, where 39% were 50 cm tall or smaller, compared with 18% in Plot 1, (excluding *V. dulitensis*: χ^2=177.2, d.f.=1, P<0.001). The difference was greater for even smaller seedlings: in Plot 2, 13.7% were less than 25 cm tall, compared to only 2.6% in Plot 1.

Proportions of small seedlings varied widely between species in both plots. *V. dulitensis* was the most extreme: almost 90% of its seedlings were less than 50 cm tall. Next highest in Plot 1 were *S. argentifolia*, with 41% smaller than 50 cm, and *P. malaanonan* (32%). Lowest proportion was in *S. fallax* (4.4%), whereas small seedlings made up 21% of the other DRM, *S. pauciflora*. In the remaining *Shorea* species, around 10% were less than 50 cm. Proportions of small seedlings were higher in Plot 2 than in Plot 1 in every species, and exceeded 20% in all except *S. johorensis* (10%). The proportion reached almost 75% in *P. malaanonan*, and almost half in *S. parvifolia*.

2.3.3.2 Large seedlings

Overall, 11% of individuals in Plot 1 were taller than 250 cm, while in Plot 2 the figure was 6.4%, a significantly lower proportion (χ^2=18.9, df=1, P<0.001). In most species in Plot 1, more than 10% of individuals were taller than 250 cm tall. *P. malaanonan* and *V. sarawakensis* had fewer than 5%, and *V. dulitensis* less than 1%. The greatest proportions of tall saplings were in the Red and Light Red Merantis: *S. leprosula* (21%), and *S. johorensis* and *S. parvifolia* (both 13%). In almost all species, proportion of large saplings was lower in Plot 2 than in Plot 1. The proportions were again highest in *S. leprosula* (22%), with *S. fallax* next (13.5%). The paucity of large saplings was again notable in *V. sarawakensis* and *P. malaanonan*, which, together with *S. argentifolia* all had less than 2.5% large saplings (Figure 2.4).

2.3.4 Species composition of the tallest seedlings

Species compositions of the tallest seedlings at the final enumeration in the two plots are given in Figure 2.5. In Plot 1, 200 individuals were included, and in

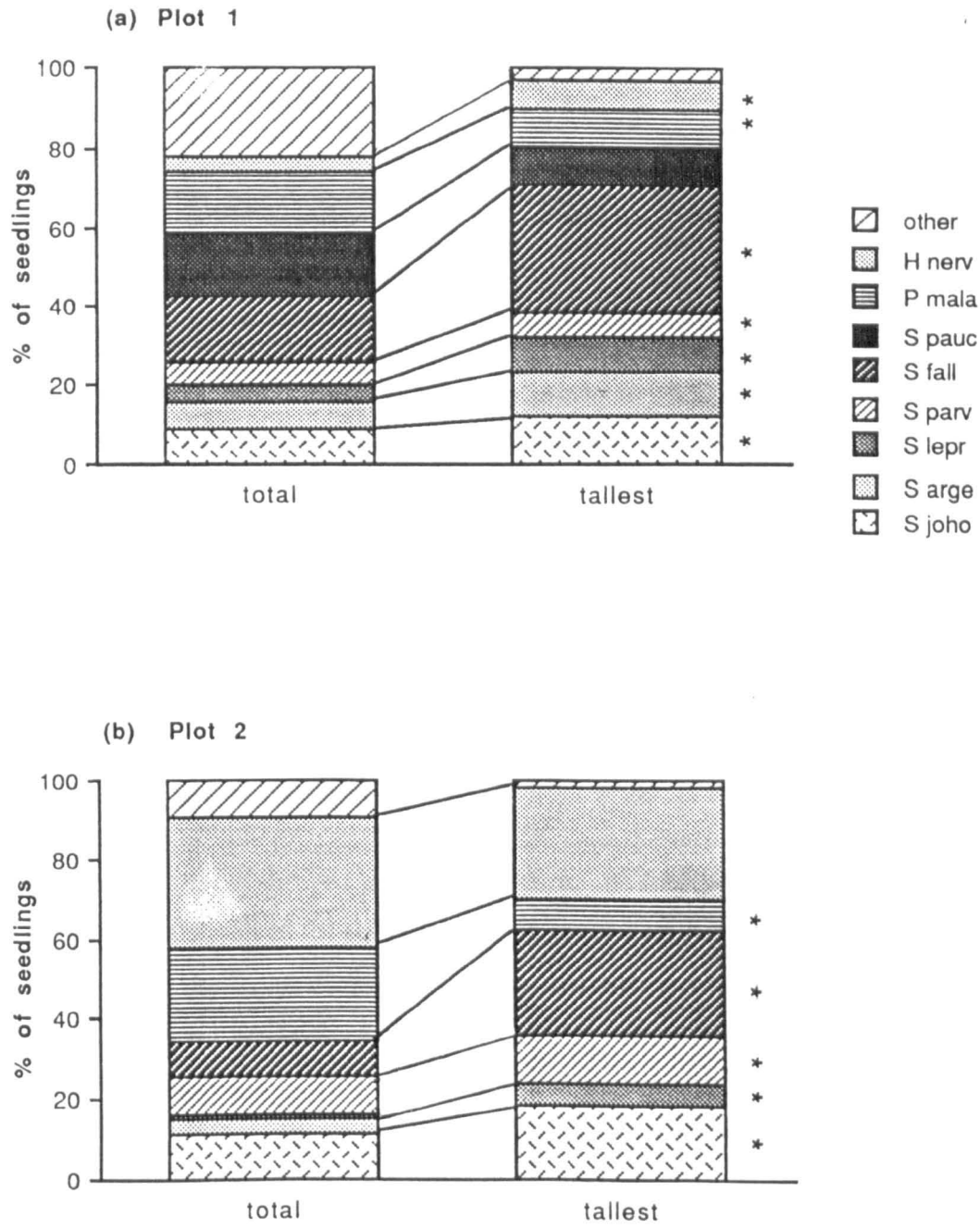


Figure 2.5
Comparison of species composition of the tallest seedlings in each plot with the overall species composition. N=200 and 50 in (a) Plot 1 and (b) Plot 2 respectively (approximately 5% of seedlings in each plot). A star (*) beside a species indicates that its proportion in the tallest group was significantly different from its proportion in the whole plot (χ^2 goodness-of-fit test comparing observed with expected number, df=1, $p<0.05$). (1985 *V. dulitensis* cohort was excluded.)

Plot 2, 50, representing around 5% of the total seedling population in each plot. Species composition of the tallest 5% clearly reflected the differences between species in the proportion of tall saplings (previous section): species with above average proportions of tall saplings were over-represented among the tallest 5% (i.e. the frequencies were higher than would be expected from a random draw from the total plot frequencies). In both plots, *S. fallax* was over-represented, together with *S. johorensis* and most LRMs, except *S. argentifolia* in Plot 2, and *S. leprosula* in Plot 1. In total, the LRMs and *S. johorensis* contributed 38% and 36% to the tallest 5% in plots 1 and 2, but made up 23% and 27% respectively of the total population. *H. nervosa* was significantly over-represented among the tallest group in Plot 1, with almost twice as many tall seedlings as expected, but not in Plot 2. *P. malaanonan* was significantly under-represented in both plots.

2.3.5 Skewness of height distributions and population size

Height distributions were positively skewed in all species in both plots. Skewness is plotted against the logarithm of population size for species in the two plots in Figure 2.6.

Species in the two plots showed a similar pattern. At low population sizes (less than *ca.* 10 individuals) values for skewness are intermediate (though estimates of skewness from such small populations are not necessarily reliable). In the remaining species, skewness increased with population size, indicating that the larger populations had relatively larger proportions of small seedlings. Each plot had a single outlier: *S. fallax* in Plot 1 and *H. nervosa* in Plot 2 both had large population sizes but low values of skewness. Excluding the species with less than 20 individuals, the rank correlation between skewness and population size was significant in both plots (Plot 1: r_s=0.65, n=11; Plot 2: r_s=0.89, n=7; P<0.05 in both).

2.4 SEEDLING CONDITION

This section describes the physical condition of seedlings, and details some of the observed causes of physical damage to seedlings.

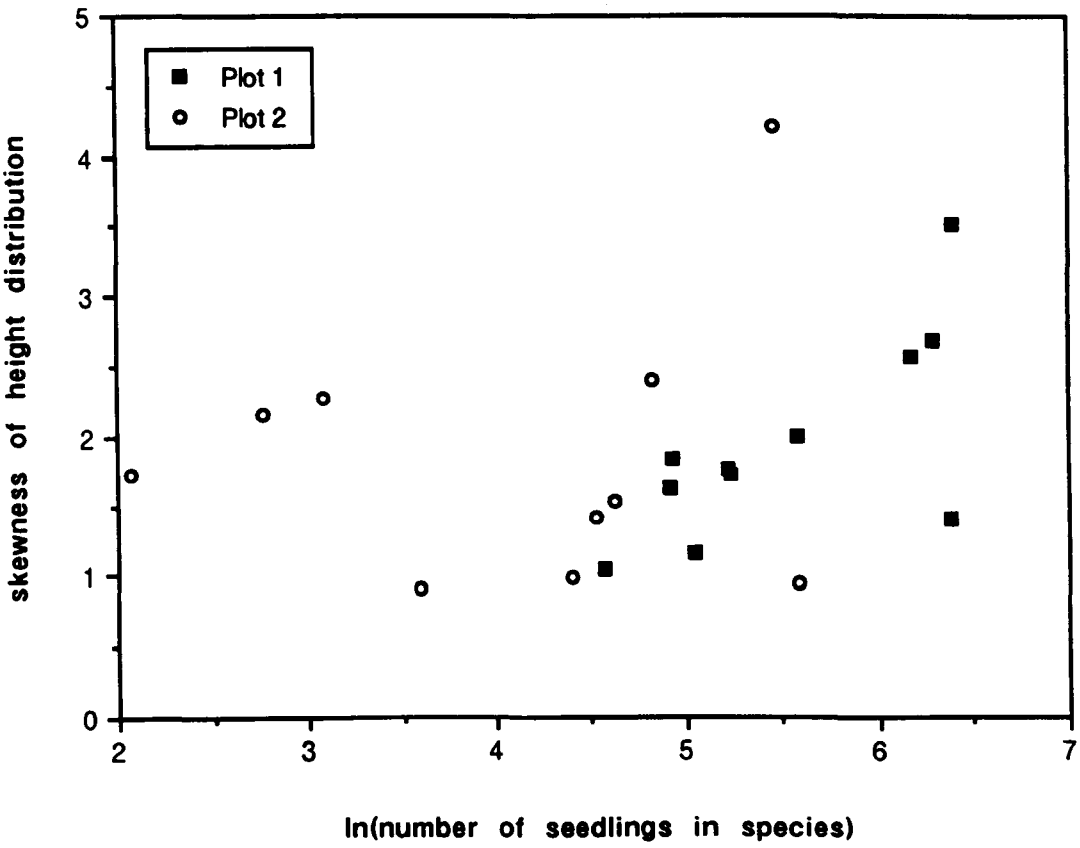


Figure 2.6 Relationship between numbers of seedlings and skewness of height distribution in Plot 1 and 2.

2.4.1 Leaf damage

Four main types of damage were observed: galls, leaf-rolling, shoot-boring and various types of leaf chewing and cutting which caused loss of leaf area. Types of damage were usually specific to a single species. Large (2 cm diameter) prickly galls were found occasionally on *S. fallax*, usually on the apical shoot. *V. dulitensis* had smaller galls (*ca.* 2 mm), maroon and velvety in texture on leaves and petioles, and *P. malaanonan* had similar sized smooth grey galls on the petioles. Leaf-rolling insects (unidentified) were observed to attack only *P. malaanonan*. *S. pauciflora* seedlings were affected by shoot-borers which entered the stem below the apical bud, causing swelling of the stem and often causing death of the apical bud. Leaf cutting insects (probably Hymenoptera) often removed large parts from the margin of young leaves in *S. argentifolia* and *S. agamii*. All species showed a variety of shapes and sizes of leaf holes, but no attempt was made to distinguish or quantify them. Despite the ubiquity of leaf herbivory, herbivorous invertebrates were very rarely observed on the leaves.

2.4.2 Apex condition

The frequencies of seedlings in each species with a dead or missing apex are shown in Figure 2.7. The total frequencies of seedlings with dead apices were similar in the two plots, 12.9% to 13.6% (final enumeration: χ^2=0.14, P>>0.05). Variation was greater between species, in Plot 1 ranging from 3% in *S. leprosula* to 26% in *H. nervosa*. Red and LRMs had fewer seedlings with a dead or missing apex than other species (Figure 2.7). In plot 2, frequency of apex loss ranged from zero (*S. leprosula*) and 2.4% (*S. argentifolia*) to 36% in *V. sarawakensis*.

2.4.3 Stem damage

A large proportion of seedlings showed signs of previous stem damage or breakage. At the final enumeration, 43.7% of seedlings in Plot 1 and 48.2% in Plot 2 had scarred stems. There was no difference between plots in the numbers of seedlings with scarred stems (χ^2=1.03, df=1, P>0.05). The proportion of seedlings with

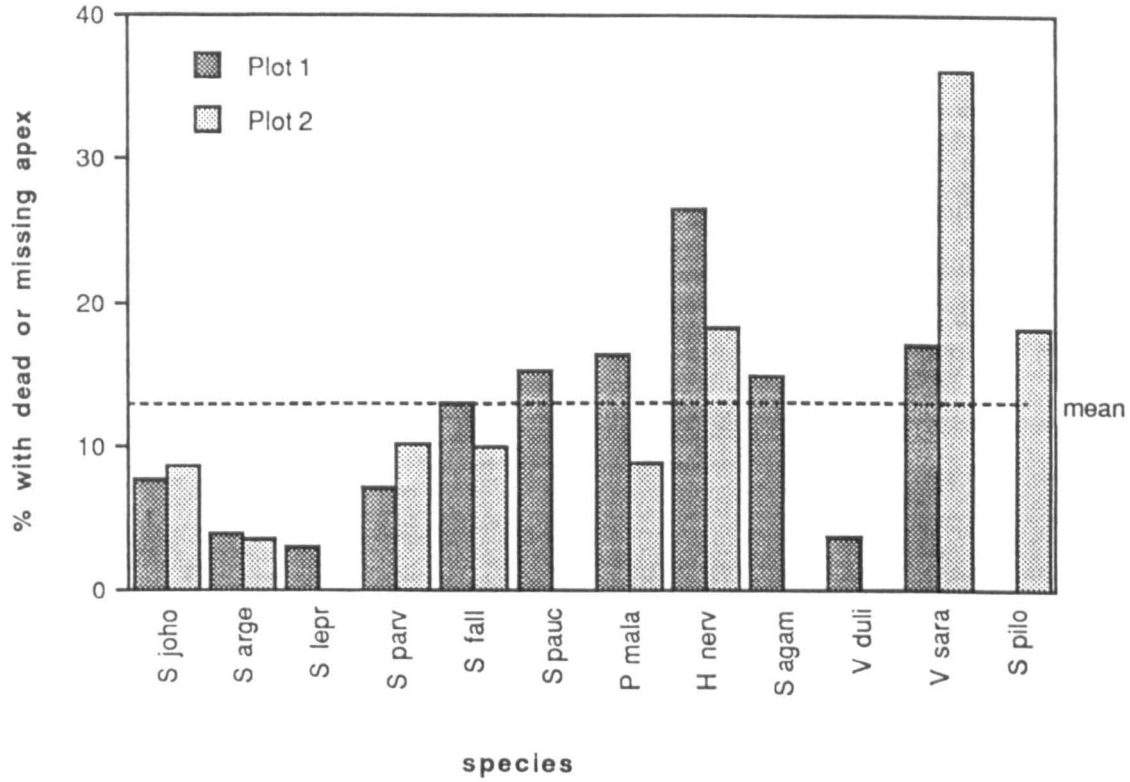


Figure 2.7 Comparison of the proportion of seedlings in each species with a dead or missing apex in Plots 1 and 2 (data from the final enumeration).

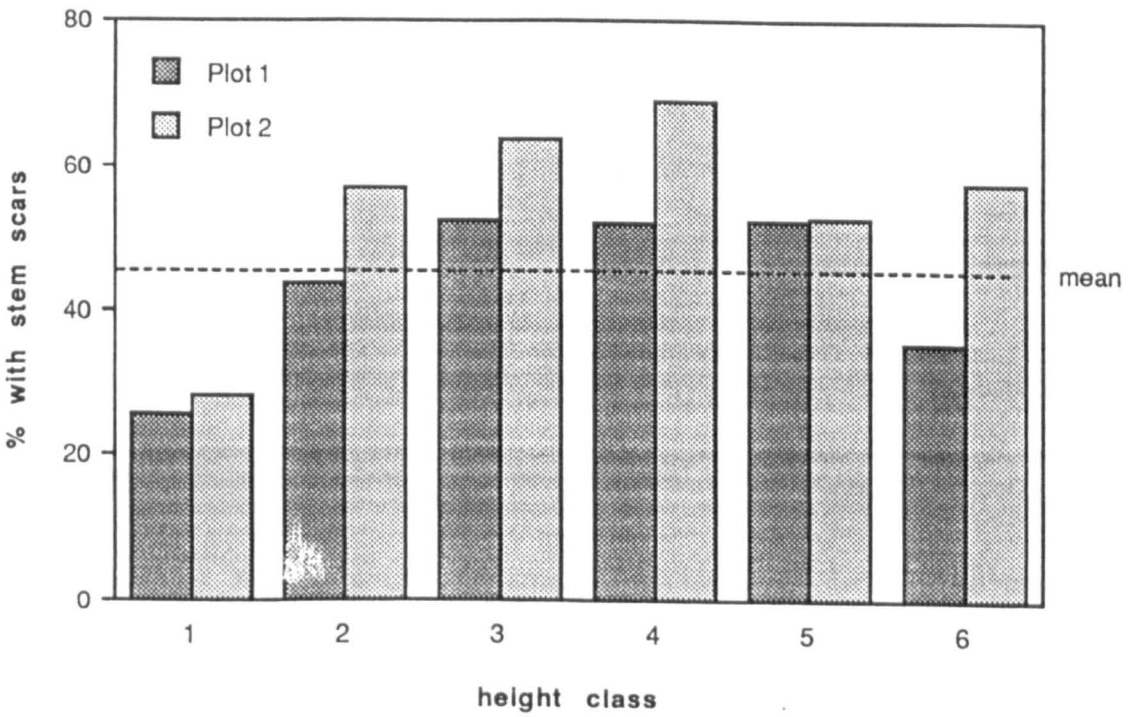


Figure 2.8 Variation with size in the proportion of seedlings with stem scarring from previous damage or breakage in Plots 1 and 2 (data from the final enumeration). Height classes 1-4 are 50 cm intervals; 5, 200-300 cm; 6, >300 cm.

scarred stems increased with seedling size (Figure 2.8): physical damage accumulated over time. On larger stems it is likely that diameter growth could hide evidence of past stem damage.

8.1% (Plot 1) and 7.0% (Plot 2) of seedlings at the final enumeration had lianes round the stem. Presence was independent of species. Frequency of lianes increased with size for all species pooled. For seedlings over 200 cm tall, 20% of seedlings had lianes around the stem in both plots.

2.5 NUMERICAL RELATIONSHIPS BETWEEN SEEDLINGS AND TREES

Examination of variation in proportions of each species in different size classes could suggest possible future changes in canopy composition, and highlight differences between species in the success of regeneration - are the major canopy species regenerating?

2.5.1 Relationship between numbers of seedlings and trees

The relationship between the number of large trees (≥60 cm gbh) and number of seedlings in each species is illustrated in Figure 2.9. Each point represents a species (log transformed numbers within each plot), and regression lines were found for each plot separately. There was a significant relationship between numbers of trees and seedlings in Plot 2 (R^2=65.0%, $P<0.05$), but not in Plot 1 (R^2=29.5%, $P>0.05$) where two species with one large tree each, *S. agamii* and *V. dulitensis*, had a higher than average number of seedlings.

2.5.2 Relationship between 'advance regeneration' and numbers of trees

The stock of large saplings and small trees has been termed 'advance regeneration' (Hubbell 1980). These were defined here as saplings and trees between 2.5 m tall and 30 cm girth (corresponding approximately to between 1 and 10 cm

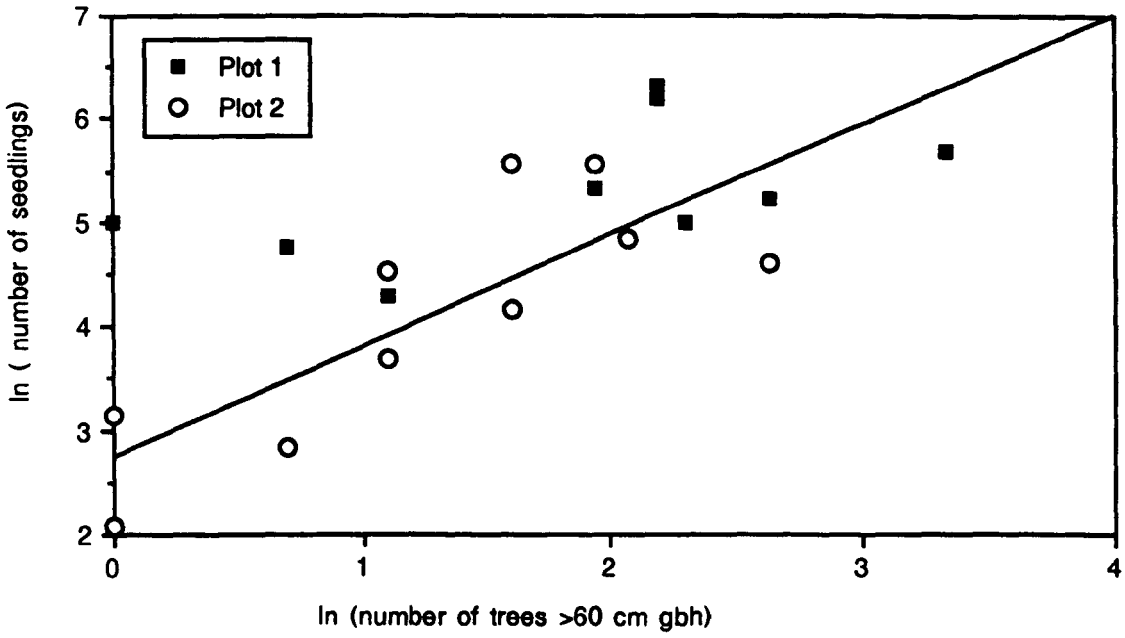


Figure 2.9 Relationship between numbers of seedlings and trees over 60 cm gbh in different species in Plots 1 and 2. The regression was significant in Plot 2 (R^2=.65, P<0.05).

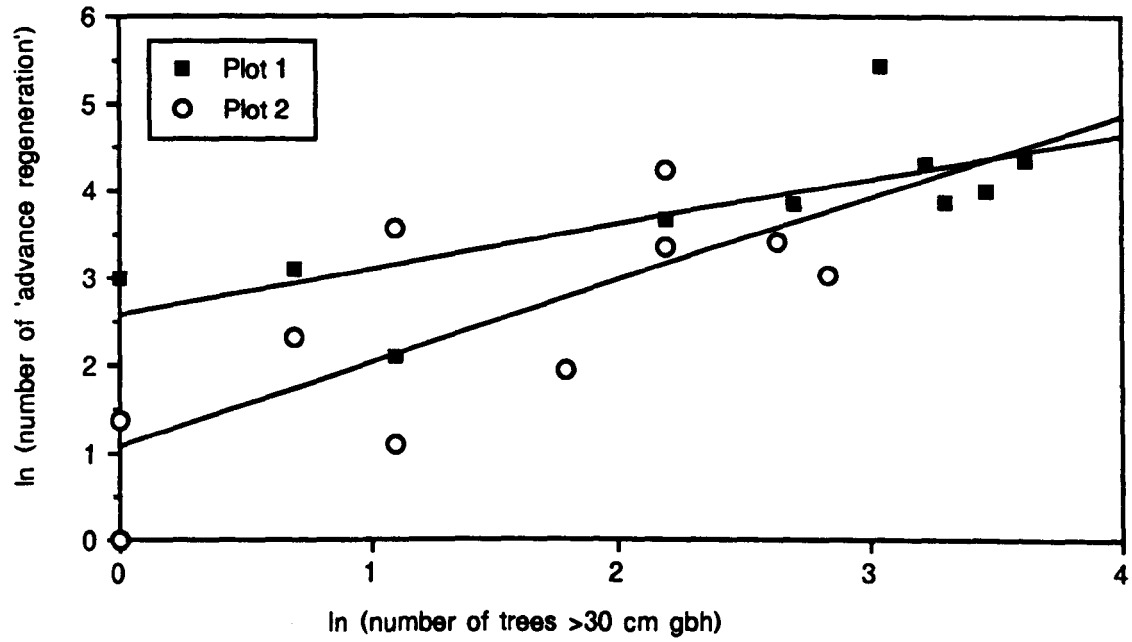


Figure 2.10 Relationship between numbers of trees over 30 cm gbh and 'advance regeneration' (seedlings and trees between 250 cm tall and 30 cm gbh) in different species in Plots 1 and 2. The regression was significant in Plot 1 (R^2=.72, P<0.001) and Plot 2 (R^2=.42, P<0.05).

dbh).

The relationship between number of trees over 30 cm girth and numbers of advance regeneration in plot 1 is shown in Figure 2.10. The regression was highly significant (R^2=72.3%, P<0.001) in Plot 1, and significant in Plot 2 (R^2=41.7%, P<0.05). The regression coefficients did not differ significantly from 1.0 (Plot 1: t=-0.515, df=9; Plot 2: t=-0.394, df=7; P>0.5 in both plots), indicating that the relationship between numbers of trees and abundance of advance regeneration did not change over the range of tree abundance. In other words, the common species had the same proportion of advance regeneration as rarer species. The four dominant emergent species in the study area of Plot 1 (*S. johorensis*, *S. leprosula*, *S. parvifolia* and *S. pauciflora*) formed a discrete group (Figure 2.10).

2.5.3 Variation in species composition with size

Dominance of each species within a size class was defined as its percentage contribution to the total number of individuals (dipterocarps only) in the size class. Seedlings were split into six height classes (50 cm intervals up to 2 m, 2-3 m, >3 m) and trees into five girth classes (10.0-29.9 cm, 30.0-59.9 cm, 60.0-99.9 cm, 100.0-199.9 cm, ≥200 cm). In Plot 1, seedlings and adults within the 2 ha study area were included. In plot 2, adults were included in the study area and within an additional 20 m wide border area (to give a large enough sample size), giving a total area of 1.2 ha of trees. The species composition of the larger size classes will be influenced by species stature: the canopy species such as *H. nervosa* and *Vatica* spp. never reach the same size as the emergent *Shorea* species. Variation in species composition through increasing size classes is illustrated in Figure 2.11 for nine species in Plot 1 and nine in Plot 2.

In Plot 1, the eight species showed quite different patterns. *S. fallax* was strikingly dominant over the range from saplings 1.5 m tall through to trees up to 30 cm gbh, making up over 30% of these size classes. The other species were present in similar abundance, ranging from 5 to 12%. Both above and below this central range, there were large fluctuations in dominance with size. *P. malaanonan* was the most abundant species in the smallest size class, forming 35% of seedlings less than 50 cm tall, but its dominance rapidly decreased with increasing size class. *S. argentifolia* and

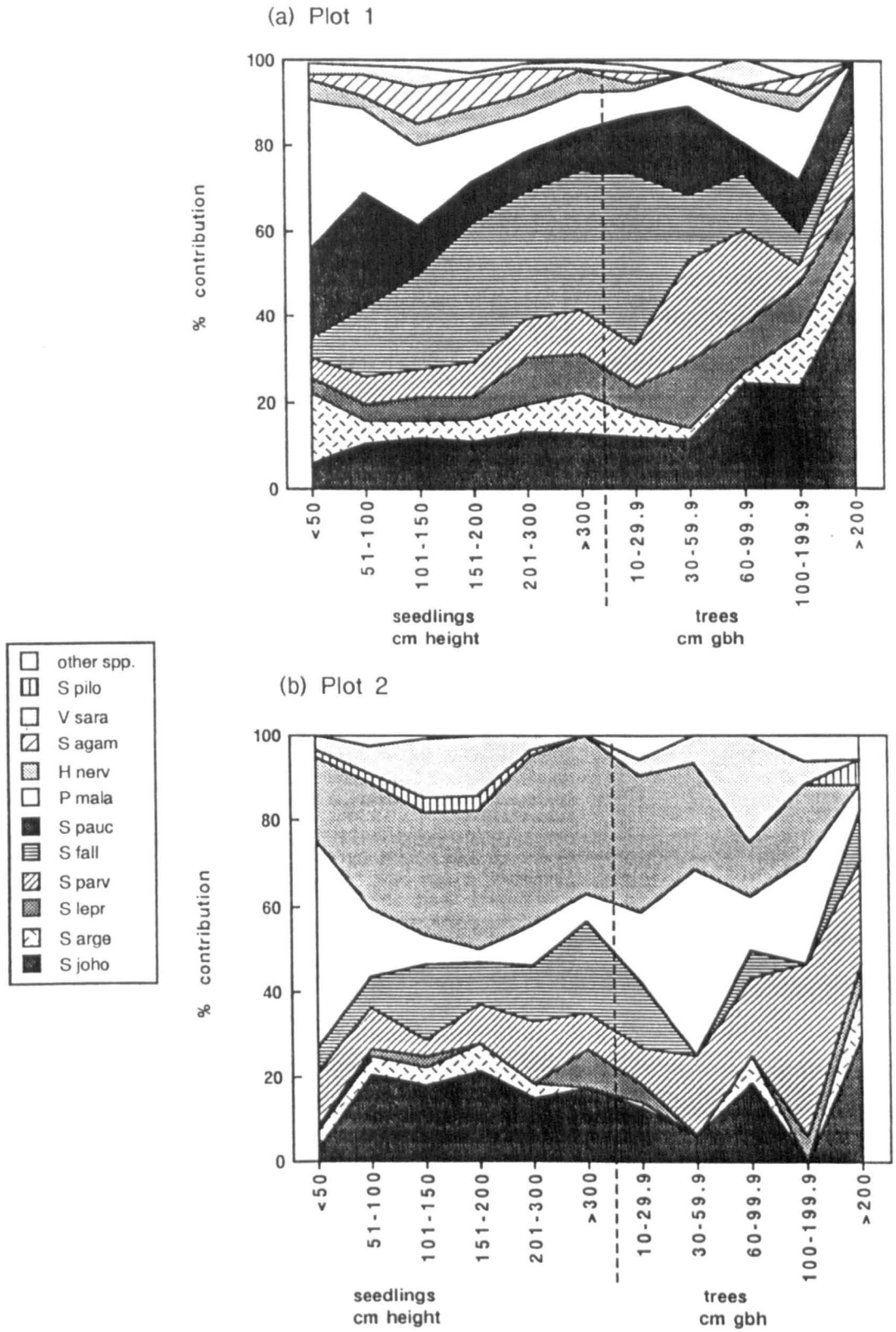


Figure 2.11 Variation in species composition in six height classes of seedling and five girth classes of tree (abscissa) in (a) Plot 1 and (b) Plot 2.

S. pauciflora were also prominent amongst small seedlings.

The LRMs and *S. johorensis* had very similar patterns: a gradual increase in dominance through the seedling size classes. The two DRMs had opposing trends over the seedling classes: *S. fallax* increased in dominance while *S. pauciflora* decreased. *S. fallax* rapidly decreased in importance from its peak in trees over 30 cm gbh (40%), and made up only 2% of the largest size class (≥200 cm gbh). *S. johorensis* became increasingly dominant to form 40% of large trees. *P. malaanonan* increased in importance to peak in trees between 100 and 200 cm gbh, but had no trees over 200 cm gbh. *S. parvifolia* peaked in importance in the two classes from 30 - 100 cm gbh, and was the most abundant species of small tree (<30 cm gbh), contributing 25%, dropped in abundance in larger trees, and was the second most abundant large tree (13%). *S. argentifolia* increased in importance over the largest two size classes, but was the least abundant *Shorea* species in all smaller size classes of trees. *S. leprosula* increased in frequency over the medium tree size classes, then decreased in importance to form less than 9% of the largest class. The six *Shorea* species made up all the large trees (≥200 cm gbh), 72% of trees 100 to 200 cm girth, and 80-88% of each of the smaller tree size classes.

In Plot 2, *H. nervosa* dominated all seedling size classes except the smallest, increasing in dominance in larger seedling size classes, but its contribution declined rapidly in the tree size classes. *P. malaanonan* showed the opposite trend: it made up almost half of all seedlings under 50 cm, but rapidly decreased in importance, increasing again to a peak in trees 60-100 cm gbh. *S. johorensis* decreased in dominance over the seedling classes, and increased again in larger trees, forming almost a third of trees over 200 cm gbh.

Most species showed broadly similar patterns of changes in dominance with size in the two plots. *P. malaanonan* was characterised by a sharp decrease in importance in seedling size classes, and a further peak in 30-60 cm trees. *S. argentifolia* occurred in similar proportions in most size classes, but increased in importance in the largest trees. *S. parvifolia* in both plots peaked in importance in medium-sized trees, 30-100 cm, and made up a large proportion of the biggest trees. Though more abundant in Plot 1, *S. fallax* in both plots contributed most to medium and large saplings and small trees, and was much less dominant among larger trees. Similarly, *H. nervosa*, which dominated the seedling classes in Plot 2, was less important in the tree classes in both plots. *S. johorensis* showed a similar rise in

dominance in larger trees in both plots, though in Plot 2, dominance of the largest tree class was shared with *S. parvifolia*.

2.6 DISCUSSION

Seedling density

Dipterocarp seedling densities fluctuate greatly over time due to mast fruiting followed by rapid mortality of small seedlings (Wyatt-Smith 1966, Fox 1972, Ashton 1982). The great variation in seedling density between forests types in Sabah has been highlighted by Fox (1972, 1973), who also stressed the variation within forest types. Limited efficiency of seed dispersal contributes to patchiness on a smaller scale.

Widely differing estimates of dipterocarp seedling densities in Sabah have been reported, usually based on milliacre sampling, for example by Fox (1967, 1972, 1973) and Liew & Wong (1973). Liew & Wong (1973) give densities of 25 - 49 thousand seedlings per hectare as typical of lowland dipterocarp forest in Sabah, and report that Tawau Hills F.R. is "comparatively low in dipterocarp seedlings" with a density of 7370 ha^{-1}. Fox (1972) reports seedling densities at Sepilok of between 14 and 57 thousand per hectare. The overall picture is of considerable variation, both in time and space. However, the densities of dipterocarp seedlings in the Danum plots, at about 2000 ha^{-1} seems low compared with most reports.

Species composition

The forests of eastern Sabah are known to be abundant in seedlings of *P. malaanonan* and *S. johorensis* (Liew & Wong 1973). They report densities of *P. malaanonan* seedlings between 1331 ha^{-1} and 46000 ha^{-1}, and of *S. johorensis* seedlings, 309 to 11660 ha^{-1}, in a variety of forest types. At Sepilok, densities of *S. johorensis* seedlings were 11753 ha^{-1} ±4691 (Fox 1967). Once more, this emphasises the huge

variability in seedling numbers. In the Danum plots, *P. malaanonan* was overall the most abundant species of seedling, with mean density of 350 ha^{-1} (Plot 1: 294 ha^{-1}; Plot 2: 583 ha^{-1}). *S. johorensis* was the sixth most abundant species, at densities of 166 ha^{-1} and 279 ha^{-1} in the two plots.

Height distributions

There was considerable variation between species in height frequency distributions and in the proportions of small (≤50 cm tall) and large (>250 cm tall) seedlings. In the slow-growing species (especially *V. sarawakensis*), multiple peaks were present in the height frequency distributions. It is tempting to suggest that the peaks may represent separate cohorts, with spacing between recruitment events being maintained by uniform and slow growth rates in these species.

Apart from the special case of *V. dulitensis*, which fruited the year before the study began, no fruiting had been recorded for the previous three years. The smallest seedlings recorded had therefore survived at least three years. Differences between species in the proportion of small seedlings may therefore indicate varying ability of small seedlings to survive without growing in closed forest. High proportions of small seedlings were found in both relatively shade tolerant species (eg. *H. nervosa* in Plot 2), and in strongly light-demanding species: *S. argentifolia* in both plots and *S. parvifolia* in Plot 2. The high proportion of small seedlings in *S. argentifolia* is surprising, given the high mortality rate in this species (Chapter 3). Of course, mortality may be high because of the high proportion of small seedlings in the population, and the survey may have recorded the last survivors of the most recent mast-fruiting. *P. malaanonan* is well known for abundant populations of small seedlings (Meijer & Wood 1964, Fox 1972); in the Danum plots, 32% and 74% (Plots 1 and 2) were less than 50 cm tall.

Differences between species in the proportion of large seedlings may indicate differing ability to grow under low light levels. Alternatively, seedlings may be large because they are, or were, growing in a canopy opening. Low mortality rates, or fast growth rates, could also lead to an accumulation of large saplings in the population. Highest proportions of large seedlings were found in *S. leprosula* and *S. fallax* in both plots and *H. nervosa* in Plot 2, and these species were well-represented among the

tallest 5% of seedlings in the plots. The high proportion of large *S. leprosula* seedlings is difficult to explain. Large seedlings of this species were observed to be aggregated in areas of more open canopy, where growth and survival may have been higher than in closed forest. Without measurements of the light environment of every sapling, it is impossible to say. Proportions of large seedlings were low in *P. malaanonan* and *V. sarawakensis* in both plots, and in *S. pauciflora* in Plot 1. The evidence therefore appears to point to both possibilities. High proportions of large seedlings occurred both in species with low mortality rates: *S. fallax* and *H. nervosa* in Plot 1, and those with fast growth rates: *S. johorensis* and most of the LRMs. On the other hand, *V. sarawakensis*, which had a very low mortality rate (Chapter 3) had few large seedlings. *P. malaanonan*, a species with relatively high growth rates among seedlings (Chapter 4) also had few large seedlings. The species composition of the tallest 5% of seedlings reinforces the point that under 'closed forest' conditions, light levels must be high enough, or small canopy openings frequent enough, to allow relatively high proportions of LRM saplings to be present. That there were clear differences between LRMs in the proportions of both small and large seedlings is surprising, given their similar ecology.

In summary, there was no clear association between light-demanding status and the proportions of small and large seedlings in each species. The results suggest, however, that small LRM seedlings can persist for years in closed forest, and that proportions of large seedlings in light-demanding species are not necessarily lower than in more shade tolerant species.

Height distribution and population size

Large population size could result from either: 1) low rates of mortality, which would over time lead to a build up of large saplings in the population; or 2) high fecundity, with the population periodically topped up after mast fruiting, resulting in a large numbers of small seedlings. The first scenario would result in a negatively-skewed height distribution, and the second a positively-skewed height distribution. Scenario 1 might be expected in slow-growing species with low mortality rates, such as the Dark Red Merantis, *H. nervosa* and *V. dulitensis*, while more light-demanding

species, the Light Red Merantis and *P. malaanonan*, may follow scenario 2. In both plots there was a significant relationship between population size and skewness of height distributions indicating that the larger populations contained proportionally more small seedlings. Each plot contained a single outlying species. Both were species with large population sizes, but low values of skewness (i.e. the populations contained a lower proportion of small seedlings relative to other species): *H. nervosa* in plot 2 and *S. fallax* in plot 1. Both these species had low mortality rates.

Physical damage

The overwhelming majority of seedlings showed evidence of damage, from both biotic (leaf herbivory, stem-borers) and abiotic (stem breakage) causes. The various types of leaf damage noted appeared, within the limitations of this survey, to be species-specific. In contrast, the damage due to physical causes was more related to seedling size: the frequencies of stem breakage and lianes increased with seedling size, reflecting the longer time for accumulation of damage in larger seedlings.

High frequencies of stem breakage have been reported for other tropical species. The majority of individuals of understorey *Piper* spp. in Costa Rica had evidence of at least one broken branch (Gartner 1989). In another Costa Rican understorey species, *Faramea occidentalis*, 78% had one or more breakage scars (Calvo *et al.*, in Gartner 1989). On Barro Colorado Island, Panama, between 13% and 40% of trees over 10 cm dbh in ten 0.1 ha plots showed signs of previous stem breakage (Putz & Milton 1989). These studies all stress the importance of re-sprouting in the recovery of broken or damaged woody plants.

In dipterocarp seedling populations, evidence from the present study suggests that physical damage is more important than herbivory in causing loss of biomass, and occurred in a large proportion of seedlings in the present study. Defence against this type of damage is impossible, so there is likely to be selective pressure for regrowth. Young saplings of *Shorea robusta* in Himalayan foot-hills die back repeatedly after severe frost until the root-stock has accumulated sufficient nutrients to produce shoots which can survive the winter stress (Rao & Singh 1985). Regrowth has been suggested as an alternative to chemical defence as a strategy to cope with

herbivore pressure in biennial species (Meijden *et al.* 1988). The hypothesis predicts that root-shoot ratio and regrowth should be positively correlated.

Re-sprouting has been studied in dipterocarp seedlings by Ng (1976). In seedlings of many dipterocarp species, the plagiotropic lateral shoots develop from non-dormant axillary buds at the same time as the subtending leaf. These branches (termed sylleptic branches) are distinct from the branches which can develop from dormant axillary buds lower down the stem. When the leading shoot is lost, a new orthotropic leader must develop quickly to maintain height growth. If a lower lateral branch becomes orthotropic, the stem would have a distinct bend, weakening the trunk. If one of the lower dormant axillary buds becomes the new leader, there will be a large die-back. Instead minute accessory buds, present in each axil, can become the new leader. In experimental decapitation of 30 seedlings of *S. platyclados*, the accessory bud in the highest axil developed to form a single new leader in all seedlings (Ng 1976). In contrast to the other axillary bud, which is plagiotropic and free of apical dominance, the accessory bud is under complete apical dominance and is orthotropic so that if the leading shoot is damaged, a new leader can quickly take over and continue height growth. The advantage of the accessory bud is clear in seedlings subjected to a high risk of physical damage to the stem. Other dipterocarp species known to possess accessory buds include *S. leprosula*, *S. parvifolia* and possibly *P. malaanonan* (Ng 1976), all relatively fast-growing species.

Relationship between numbers of trees and seedlings

One much repeated view of regeneration in tropical forests is Aubréville's Mosaic Theory (Richards 1952): Aubréville (1938) noted in West African forests that some species in the upper canopy were poorly represented in the understorey, and that patches of juveniles of canopy trees occurred in areas where those trees were absent from the canopy. Later observations by Jones (1955) supported this view, but this phenomenon may be confined to West Africa (Swaine & Hall 1988). In Malaysia, Fox (1972) notes at Sepilok that, among the dipterocarps, the "more abundant species as big trees have highest seedling populations". Manokaran (1988) found that for all species in the 2 ha plot at Sungei Menyala, 40% were present as saplings (1.5 m tall

to 10 cm dbh) within a 0.08 ha subplot. Species composition of trees 30 cm dbh and over remained "remarkably constant" over 38 years, although over half the original trees had died and been replaced.

In the Danum plots, there was a significant positive relationship between number of large trees and numbers of both seedlings and advance regeneration. The species dominating the canopy and emergent trees were well-stocked in the understorey as saplings and small trees. The changes in dominance over size classes in the Danum plots were greatest in small seedlings and in trees over 30 cm gbh. Large changes also occurred in the larger trees, over 1 m girth, but changes in percent contribution are magnified by the small numbers in these size classes, and by the fact that some species rarely reach this size. Swaine & Hall (1988) used ordination methods to analyse compositional variation through size classes in different forest types in Ghana. They found large variations in species composition between size classes, but there was no consistent pattern: the size classes in which change occurred varied between forests.

The present analysis emphasises the dominance of *S. johorensis* among the biggest trees. Proportions of *S. parvifolia*, *S. leprosula*, *S. pauciflora* and *P. malaanonan* were higher in medium-sized trees. In smaller trees, *S. fallax* was very dominant. The stability and equality in species composition from medium-sized saplings to small trees in Plot 1 is surprising, because over this range growth rates are very variable. Trees either grow rapidly into the canopy, or grow slowly and remain suppressed in the lower canopy (van Steenis 1956, Nicholson 1965). It cannot be assumed however that the composition of smaller trees will be a good indicator of future canopy composition. Growth rates can vary enormously in small trees within the same species and size range (eg Wyatt-Smith 1958, Nicholson 1965, Lieberman *et al.* 1985a, Manokaran 1988, Welden *et al.* 1991). Additionally, trees of this size are able to remain suppressed for varying, often long, periods of time (see Swaine *et al.* 1987). Combined with the random nature of gap creation, which is important in releasing small trees to grow into the upper canopy, these variables lead to unpredictability of future canopy composition (Swaine & Hall 1988).

CHAPTER 3

MORTALITY OF SEEDLINGS

3.1 CALCULATION OF MORTALITY RATES

3.1.1 Choice of model

Mortality rates were described by the logarithmic model. This assumes that a constant proportion of individuals die over any time interval, resulting in a logarithmic decline in numbers over time. The calculated mortality rate is independent of the time interval between enumerations, and is therefore suitable for calculation of mortality rates over unequal time intervals. This pattern of mortality gives rise to the logarithmic decrease in tree numbers with increasing size, characteristic of forests in equilibrium. Log model mortality rates have been applied in demographic studies of tropical trees (Swaine & Lieberman 1987) and seedlings (Clark & Clark 1989).

The equation is:

$$m = 100 (\ln n_0 - \ln n_1) / t$$

where t is time in years between enumerations, n_0 is the number of individuals present at the beginning, and n_1 the number surviving to the next enumeration (Causton 1983).

While the assumption of constant mortality in any size class does not hold for the smallest seedlings (Section 3.4), the linear model (annual percent mortality), calculated from:

$$m = 100 (n_0-n_1) / n_0 . t$$

implies that mortality is increasing over time (ie. that the proportion of survivors dying in any time interval is increasing); in addition, the calculated rate is not independent of the time interval between enumerations (Swaine & Lieberman 1987).

The linear model has been used in previous studies of dipterocarp seedling mortality (eg. Liew & Wong 1973, Becker 1983) and is presented here to allow comparison with these studies. Mortality rates discussed below are based on the log model, unless stated otherwise.

The half-life of a population, $t_{0.5}$, (time for initial population to halve in numbers) can be calculated from the log mortality rate, m (Swaine & Lieberman 1987):

$$t_{0.5} = \ln(0.5) / 0.01m$$

3.1.2 Calculation of inter-census interval

The first enumeration of Plot 1 seedlings lasted nine weeks, with effort concentrated at the beginning and end of the period, and this complicated the calculation of the time interval between the first and second intervals. The plot was surveyed systematically from south to north, so that enumeration of a species clustered near the northern end of the plot would have been completed several weeks later than a species concentrated at the southern end. Time elapsed between the first and second census would therefore differ between species, potentially introducing bias into the calculation of species mortality rates. Numbers of seedlings enumerated in each of the nine weeks, tabulated by species, are given in Appendix 4, together with modal, median and mean dates of enumeration for each species. Mean date (week) for each species (or other grouping) was found by summing the week of enumeration for each individual in the group and dividing by the total number. Modal and median values were strongly influenced by the concentration of survey effort at the start (week 0) and end (weeks 6 to 8), (Appendix 4), and were the same in all but four species. In three of these, the mean fell between median and mode. Mean date was therefore chosen as the most appropriate estimate of starting date to overcome the bias.

The second enumeration of Plot 1 lasted three weeks, (weeks 26 to 28), and mean week was again calculated as described. Average time elapsed between the first two enumerations calculated in this way ranged from 19 to 26 weeks in different species. The third enumeration took less than two weeks (weeks 100 to 101), and the date was set to week 100 for all individuals. The second and third enumerations were around 72 weeks apart, and the overall interval (first to third enumeration) was 92 to 100 weeks.

In Plot 2, the first enumeration of the majority (63%) of individuals was completed within one week (week 10). As this was the modal date in all species it was used in calculations of mortality rates. The final enumeration of Plot 2 seedlings was carried out in week 104, an inter-census interval of 94 weeks.

3.1.3 Comparison between plots

In Plot 1, mortality rates were calculated over both intervals. Second interval mortality rates were calculated twice: both excluding and including the individuals first enumerated during the second survey. Comparisons between the plots are based on mortality rates of the seedlings recorded at the first enumeration, and in Plot 1 are calculated for the overall interval (first to third enumeration).

3.2 CAUSES OF MORTALITY

Because of the long periods between enumerations, a large number of seedlings had died and decomposed completely, and the likely cause of death was impossible to determine (category 'no trace'). For seedlings categorised as 'standing dead', death could have been due to shading, water or nutrient stress, pathogen attack, or a combination of causes. A proportion of seedlings died after being crushed by falling debris (category 'litter-fall'), including trees, branches, lianes, and rotting stumps. Even fallen leaves could smother very small seedlings: the 1985 cohort of *V. dulitensis*, under 20 cm height, was particularly vulnerable. The number killed in this

way is likely to be underestimated because many small seedlings had disappeared without trace.

In Plot 1, 43% of seedlings had disappeared completely (category 'no trace') between the second and third enumerations, and 27% remained as stumps. If *V. dulitensis* is excluded, the frequencies were 35% and 40% respectively. In Plot 2, 51% disappeared and 30% remained as stumps. The proportion of seedlings disappearing completely decreased with size from 53% of dead seedlings less than 25 cm height to 9% of those over 200 cm height. Larger seedlings were more likely to remain as stumps. These categories are related to size and time between seedling death and enumeration and reflect rates of decomposition. Proportions of the two categories were similar in all species ($P<0.05$) except *V. dulitensis*, in which the majority of small seedlings had disappeared completely.

3.2.1 Mortality caused by litterfall

Litterfall accounted for 11.1% (Plot 1, overall interval) and 17.4% (Plot 2) of seedling deaths over the 22 month survey. Analysis of litterfall deaths is based on aggregated data from both plots and from both enumerations in Plot 1. The total number dying as a result of litter-fall was 80 out of 668 dead seedlings, accounting for 12% of deaths, or around 2% of seedlings.

Species composition and height class frequencies of seedlings killed by litterfall are given in Table 3.1. Frequency of deaths due to litterfall were similar (range 9% to 15%) in all the major species except *S. argentifolia*, in which significantly fewer (3.1%) than expected were killed by falling litter ($\chi^2=4.19$, df=1, $P<0.05$), and *P. malaanonan*, significantly more than expected (19.3%) ($\chi^2=3.96$, df=1, $P<0.05$). In the two species (*S. pilosa* and *V. sarawakensis*) in which a single seedling died, litterfall was the cause. There were no significant differences ($P>0.05$) between size classes in the frequency of litterfall mortality, although frequency was highest in saplings 150 cm to 200 cm tall (21%).

Table 3.1 (a) Species composition and (b) height frequencies of seedlings killed by falling litter between the first and final enumerations, pooled data from Plots 1 and 2.

(a) species composition

Species	Killed by litter-fall	Total dead seedlings	% of deaths by litter-fall
S joho	10	73	13.7
S arge	2	64	3.1
S lepr	3	20	15.0
S parv	5	43	11.6
S fall	6	40	15.0
S pauc	8	72	11.1
P mala	17	88	19.3
H nerv	1	11	9.1
S agam	1	5	20.0
S pilo	1	1	100.0
V duli	25	248	12.5
V sara	1	1	100.0
Other	0	2	0.0
Total	80	668	12.0

(b) height class frequencies

Height class (cm)	Killed by litter-fall	Total dead seedlings	% of deaths by litter- fall
1 - 25	38	310	12.3
26 - 50	14	112	12.5
51 - 100	17	142	12.0
101 - 150	6	42	14.3
151 - 200	6	28	21.4
201 - 300	1	21	4.8
> 300	1	13	7.7
Total	80	668	12.0

3.3 VARIATION IN MORTALITY RATES

3.3.1 Variation between species

Numbers dying between enumerations in each species, and corresponding estimates of mortality rates (log and linear models) and half-lives are given in Table 3.2. For Plot 1, Table 3.2(a) gives mortality rates for seedlings recorded at the first enumeration, while Table 3.2(b) gives rates for the second interval for all seedlings recorded at the second enumeration (i.e. including seedlings missed at the initial enumeration). Comparison of the two estimates for second interval mortality shows little difference in the two rates.

Highest mortality was recorded in the 1985 cohort of *V. dulitensis*, with annual mortality over the first interval of 76%, giving an estimated half-life of less than one year. Over the second interval mortality decreased to 45% yr^{-1}. In contrast, mortality in the older cohorts was much lower (5.6% yr^{-1} overall), and lay within the range of the other species.

Mortality in the remaining species ranged from zero to 16% yr^{-1}. Highest mortality rates in both plots were found among the Light Red Merantis and *S. johorensis*. Annual mortality in this group ranged from 6.5% to 15.7% in Plot 1 and 3.8% to 12% in Plot 2. In Plot 1, overall mortality rates were highest in *S. argentifolia* (15.7% yr^{-1}), followed by S. johorensis (12.0% yr^{-1}). Mortality in the remaining two LRMs was half that of *S. argentifolia*, and slightly lower than in the DRM, *S. pauciflora*. Within each plot, *S. fallax* had lower mortality than the LRMs in the same plot. In Plot 2, highest mortality rates were in *S. parvifolia* (12.2% yr^{-1}), and *S. argentifolia* (9.4% yr^{-1}). Next ranked was *P. malaanonan*, with mortality of 9% yr^{-1}. Mortality in *S. johorensis* was lower than in all three LRMs.

Lower mortality rates were recorded in the canopy species. In Plot 1, no seedlings of *V. sarawakensis*, and only one seedling of *H. nervosa* died over the total period. Mortality was also low in *S. agamii* (1.9% yr^{-1}, with 5 seedlings dying). In Plot 2, *V. sarawakensis* again had a low mortality rate (0.9% yr^{-1}), with only one seedling dying. Next lowest was *H. nervosa*, with annual mortality of 2.0%.

Table 3.2 Number of seedlings dying between enumerations (1st: first interval; 2nd: second interval; tot: combined interval [weeks]), log model and annual percent mortality rates, and estimated $t_{0.5}$ (half-life) in different species and in Light Red Merantis (LRM) and Dark Red Merantis (DRM).

(a) Plot 1, seedlings recorded at first enumeration.

Species	N	Number dead			Interval		Log mortality (% yr^{-1})			Annual % mortality			$t_{0.5}$(yr)		
		1st	2nd	tot	1st	2nd	1st	2nd	tot	1st	2nd	tot	1st	2nd	tot
S joho	298	11	48	59	23.6	72.2	8.27	13.18	11.97	8.12	12.05	10.74	8.38	5.26	5.79
S arge	205	9	43	52	24.9	72.2	9.39	17.85	15.68	9.18	15.81	13.60	7.38	3.88	4.42
S lepr	149	3	15	18	23.5	72.1	4.50	7.82	7.00	4.45	7.41	6.57	15.40	8.86	9.90
S parv	186	7	14	21	24.0	72.2	8.32	5.87	6.48	8.17	5.64	6.11	8.33	11.81	10.70
S fall	564	8	22	30	21.7	71.6	3.43	2.93	3.05	3.40	2.88	2.97	20.22	23.63	22.74
S pauc	490	22	44	66	26.3	72.3	9.07	7.10	7.62	8.86	6.76	7.10	7.65	9.77	9.09
P mala	542	18	26	44	26.1	72.4	6.74	3.65	4.47	6.63	3.56	4.29	10.29	18.97	15.50
H nerv	118	0	1	1	21.2	71.6	0.00	0.62	0.48	0.00	0.62	0.47	>33.20*	112.09	145.37
S agam	146	0	5	5	24.5	72.0	0.00	2.52	1.88	0.00	2.47	1.84	>47.52*	27.56	36.94
S sp10	19	0	0	0	24.9	72.1	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-
S symi	5	0	0	0	23.6	72.0	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-
V dul1‡	515	16	33	49	20.2	72.0	8.11	4.94	5.64	7.98	4.78	5.36	8.55	14.03	12.30
V dul2‡	333	82	117	199	19.4	72.0	75.81	45.33	51.80	66.04	33.67	34.00	0.91	1.53	1.34
V sara	73	0	0	0	22.7	71.8	0.00	0.00	0.00	0.00	0.00	0.00	>21.94*	>69.39*	>91.32*
LRM & S joho	838	30	120	150	24.0	72.2	7.90	11.59	10.67	7.76	10.70	9.68	8.77	5.98	6.50
DRM	1054	30	66	96	23.8	71.9	6.30	4.82	5.19	6.21	4.66	4.95	11.01	14.39	13.37
All spp. except V dul2	3325	94	251	345	23.6	72.1	6.32	5.84	5.95	6.23	5.61	5.64	10.98	11.88	11.64
Total	3658	176	368	544	23.2	72.1	11.04	8.06	8.79	10.77	7.63	8.12	6.28	8.60	7.89

‡ V dul1 - *V. dulitensis* seedlings older than 1985 cohort
‡ V dul2 - *V. dulitensis* seedlings of 1985 cohort
* Minimum $t_{0.5}$ calculated by assuming that one seedling died during interval

Table 3.2 b) Plot 1, 2nd interval mortality rates for all seedlings recorded at second enumeration.

Species	N	Number dead	Interval (weeks)	Annual % mortality log	linear	$t_{0.5}$
S joho	313	54	72.2	13.65	12.43	5.08
S arge	226	48	72.1	17.22	15.31	4.03
S lepr	151	15	72.2	7.55	7.71	9.18
S parv	192	17	72.1	6.68	6.38	10.37
S fall	603	28	71.5	3.46	3.38	20.05
S pauc	518	50	72.4	7.29	6.94	9.50
P mala	553	30	72.4	4.01	3.90	17.31
H nerv	132	1	71.5	0.55	0.55	125.37
S agam	156	5	72.0	2.35	2.31	29.47
S sp10	19	0	72.1	0.00	0.00	-
S symi	6	0	72.0	0.00	0.00	-
V dul1‡	500	33	72.0	4.93	4.77	14.06
V dul2‡	251	117	72.0	45.33	33.67	1.53
V sara	76	0	71.8	0.00	0.00	>72.26*
LRM + S joho	882	134	72.1	11.88	10.95	5.83
DRM	1121	78	71.9	5.21	5.03	13.29
All spp. except V dul2	3462	283	72.0	6.15	5.90	11.26
Total	3713	400	72.0	8.23	7.78	8.43

‡ V dul1 - *V. dulitensis* seedlings older than 1985 cohort
V dul2 - *V. dulitensis* seedlings of 1985 cohort

* minimum $t_{0.5}$ calculated by assuming that one seedling died during interval

c) Plot 2. Interval was 94 weeks.

Species	N	Number dead	Annual % mortality log	linear	$t_{0.5}$
S joho	126	8	3.79	3.67	18.29
S arge	40	6	9.39	8.67	7.38
S lepr	17	2	7.23	6.80	9.58
S parv	100	19	12.17	10.98	5.69
S fall	93	4	2.54	2.49	27.29
P mala	262	39	9.31	8.60	7.44
H nerv	259	9	2.04	2.01	33.92
S symi	8	0	0.00	0.00	-
S pilo	23	1	2.57	2.51	26.99
V sara	65	1	0.90	0.89	77.38
LRM + S joho	283	35	7.30	7.81	9.50
Total	993	81	5.43	5.18	12.7

3.3.2 Variation between plots

Differences in mortality between plots were tested with a χ^2 test of independence to compare numbers alive and dead at the final enumeration (including only those individuals present at the first enumeration).

Mortality of all species pooled (excluding *V. dulitensis* in Plot 1) did not differ significantly between the plots (χ^2=2.35, df=1, P>0.05). Mortality of LRMs was virtually identical in the two plots (χ^2=0.01, df=1, P>0.05). In individual species, differences between the plots were significant in two species: more *S. johorensis* (χ^2=12.94, df=1, P<0.001) and fewer *P. malaanonan* (χ^2=9.17, df=1, P<0.01) died in Plot 1 than in Plot 2. Although actual values differed between plots in some species, mortality rates of the nine species common to both plots were significantly rank correlated (Spearman r_s=0.792, P<0.05).

3.3.3 Temporal variation in mortality

Mortality rates for two consecutive intervals were estimated only in Plot 1 populations. For each major species, the null hypothesis was tested that mortality in the second interval was the same as that over the first interval. The log model equation, which assumes constant mortality over time, was used to predict the number expected to die over the second interval given the observed rate over the first interval. Predicted number of deaths was compared with observed number using a χ^2 goodness-of-fit test.

Mortality rates in *S. johorensis* and two LRMs, *S. argentifolia* and *S. leprosula* were very significantly higher over the second interval than over the first (χ^2=9.14, χ^2=15.13, χ^2=4.31 respectively, df=1, P<0.05, Figure 3.1). In the remaining LRM, *S. parvifolia*, mortality in the second interval was slightly lower, though not significantly. Mortality was significantly lower over the second interval in *P. malaanonan* and the 1985 cohort, and older *V. dulitensis* seedlings (χ^2=9.34, 12.41, 9.49 respectively, df=1, P<0.01). Mortality of LRMs as a group was very significantly higher over the second interval (χ^2=15.49, df=1, P<0.001), increasing from 7.9% to 11.6% yr^{-1}. In contrast, DRM mortality decreased significantly (χ^2=4.42, df=1, P<0.05) from 6.3% to 4.8% yr^{-1}.

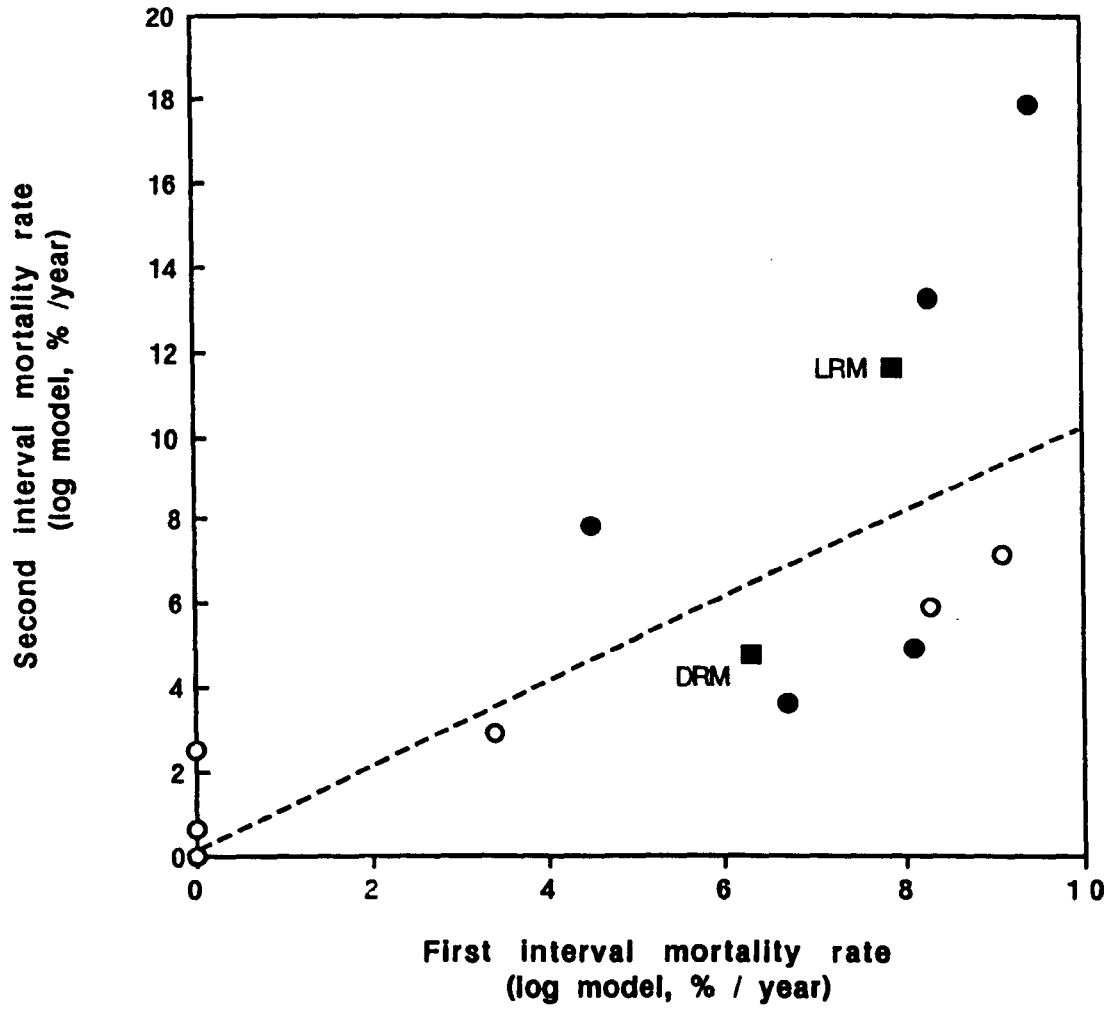


Figure 3.1 Comparison of mortality rates in the first and second intervals in different species, and in Light and Dark Red Merantis (LRM, DRM) in Plot 1. Dashed line is equal mortality in both intervals. Filled symbols indicate significant difference ($P<0.05$) between the two rates.

3.4 MORTALITY AND SIZE

3.4.1 Variation in mortality with size

Log annual mortality rates in twelve height classes for individuals in all species pooled are shown in Figure 3.2. In both plots, mortality was highest in the smallest height class (≤25 cm), and was more than double the rate of the next larger class. There was a clear step from high mortality in small seedlings to lower mortality in the larger height classes. There is a suggestion of a secondary peak in mortality in larger seedlings. In Plot 1, this peak occurred in seedlings 151-225 cm tall, and in Plot 2, seedlings greater than 200 cm.

Within each height class mortality rates were compared between plots using a χ^2 goodness-of-fit test on the numbers dead and alive in each plot. Mortality differed significantly between plots in each of the three smallest size classes ($P<0.05$), and was higher in Plot 1 in all three. Even if the 1985 *V. dulitensis* cohort is excluded, mortality was still higher in the three smallest height classes in Plot 1.

3.4.2 Variation between species in size-related mortality

Annual mortality rates in six height classes in the major species in both plots are shown in Figure 3.3. In most species in Plot 1 [Figure 3.3(a)], mortality was highest in the smallest seedlings (<50 cm height). In two species (*S. johorensis* and *S. argentifolia*) mortality peaked in seedlings 51-100 cm tall. In *H. nervosa* (not illustrated) the only death was of a sapling 175 cm tall.

The pattern of varying mortality rates with size differed between species. In Plot 1 , in the two species with highest rates (>10% yr^{-1}), *S. argentifolia* and *S. johorensis*, mortality was high in most height classes. In *S. argentifolia*, mortality was high in the smaller size classes, dropping to a lower level only in saplings greater than 200 cm. The trend in size-related mortality was less clear in *S. johorensis*: there was a sharp drop in mortality of intermediate sized (101-150 cm) saplings, and a marked secondary peak in mortality in larger saplings (151-250 cm).

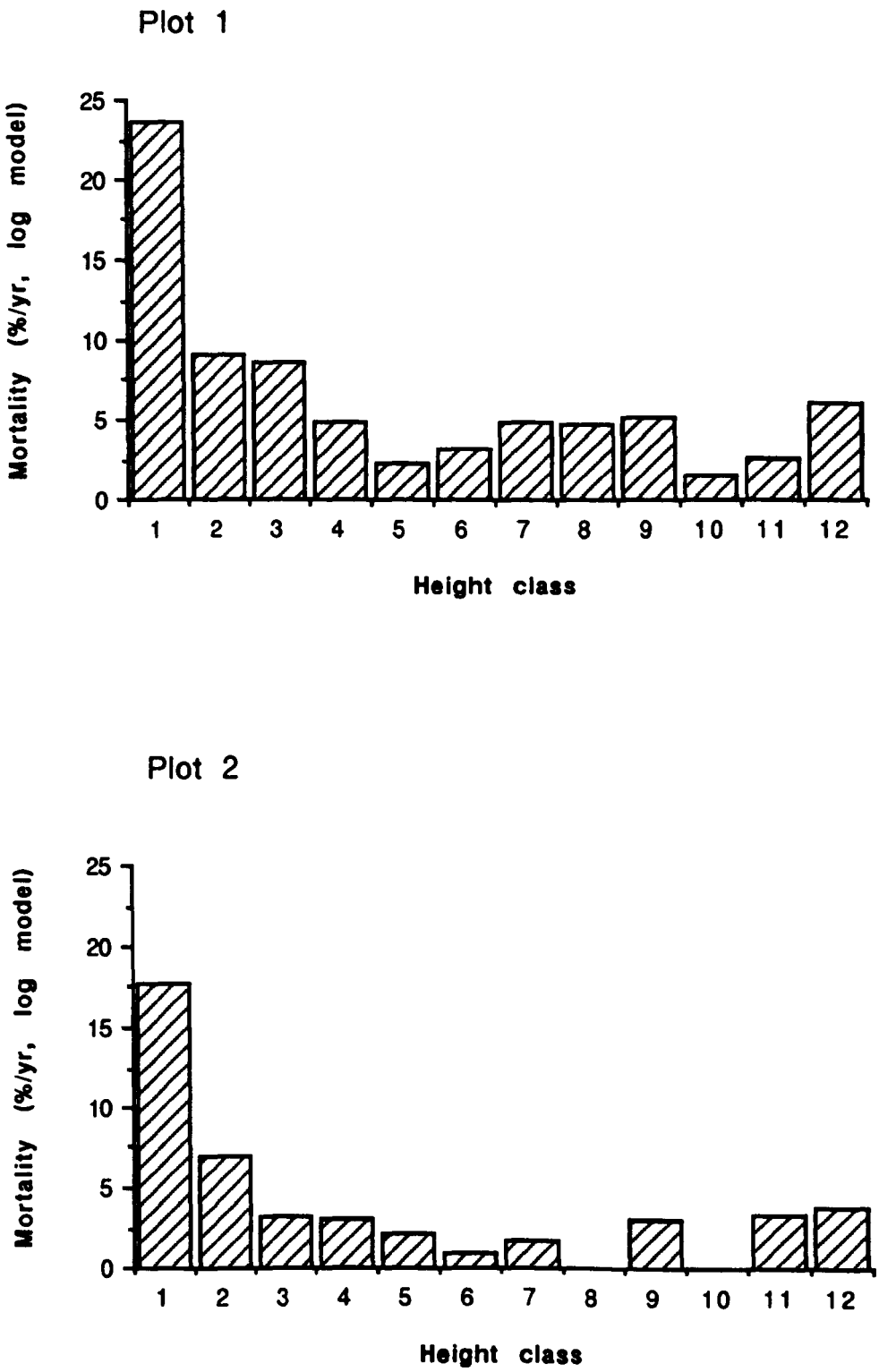


Figure 3.2 Mortality rates in twelve height classes for all species pooled in Plots 1 and 2 (excluding *Vatica dulitensis*). Height classes 1 to 10 are in 25 cm intervals; class11, 251-300 cm; class 12, >300 cm.

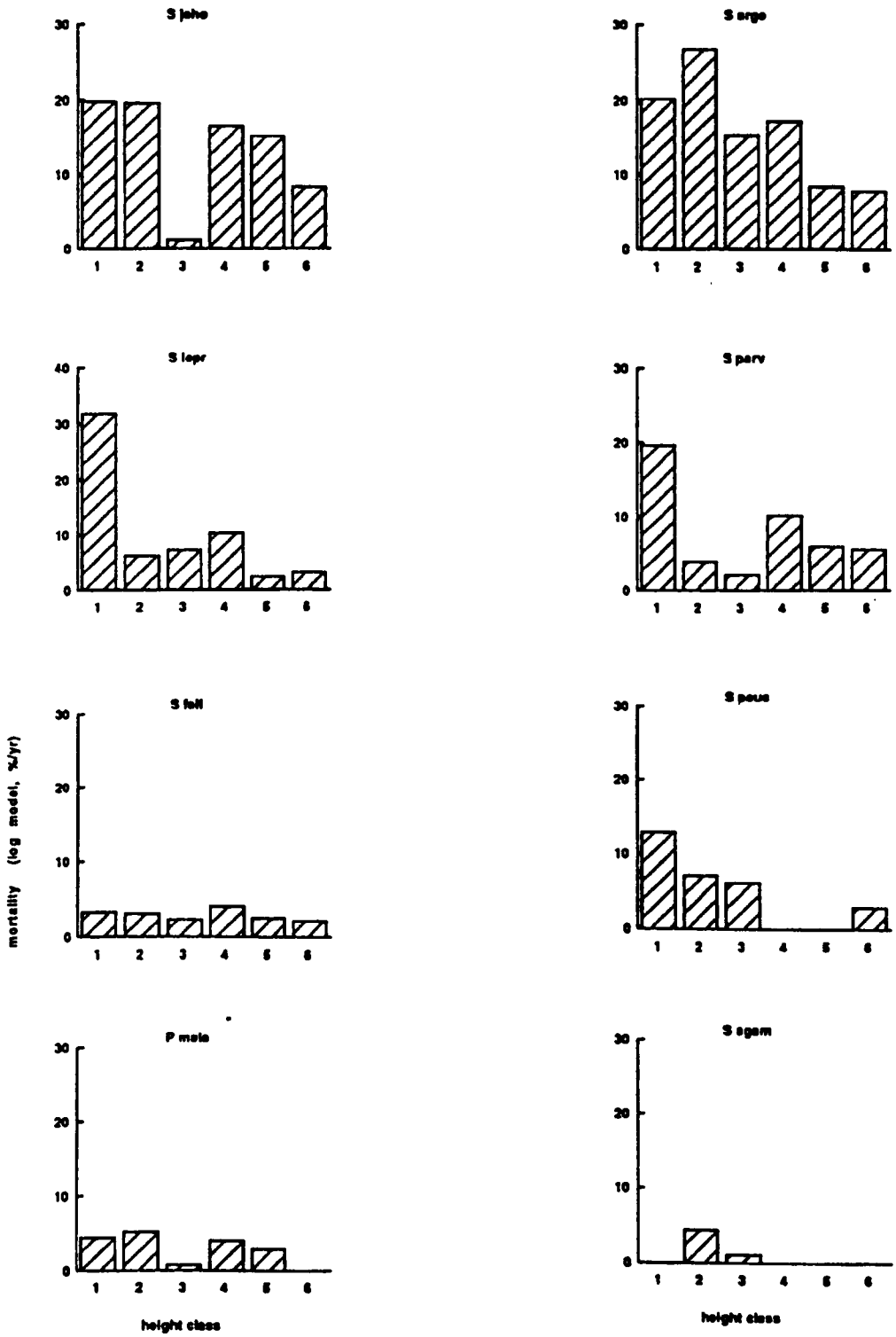


Figure 3.3 Mortality rates (%/yr, log model) in six height classes in different species. Height classes 1 to 4 are in 5o cm intervals; class 5, 251-300 cm; class 6, >300 cm.

(a) Plot 1, second interval

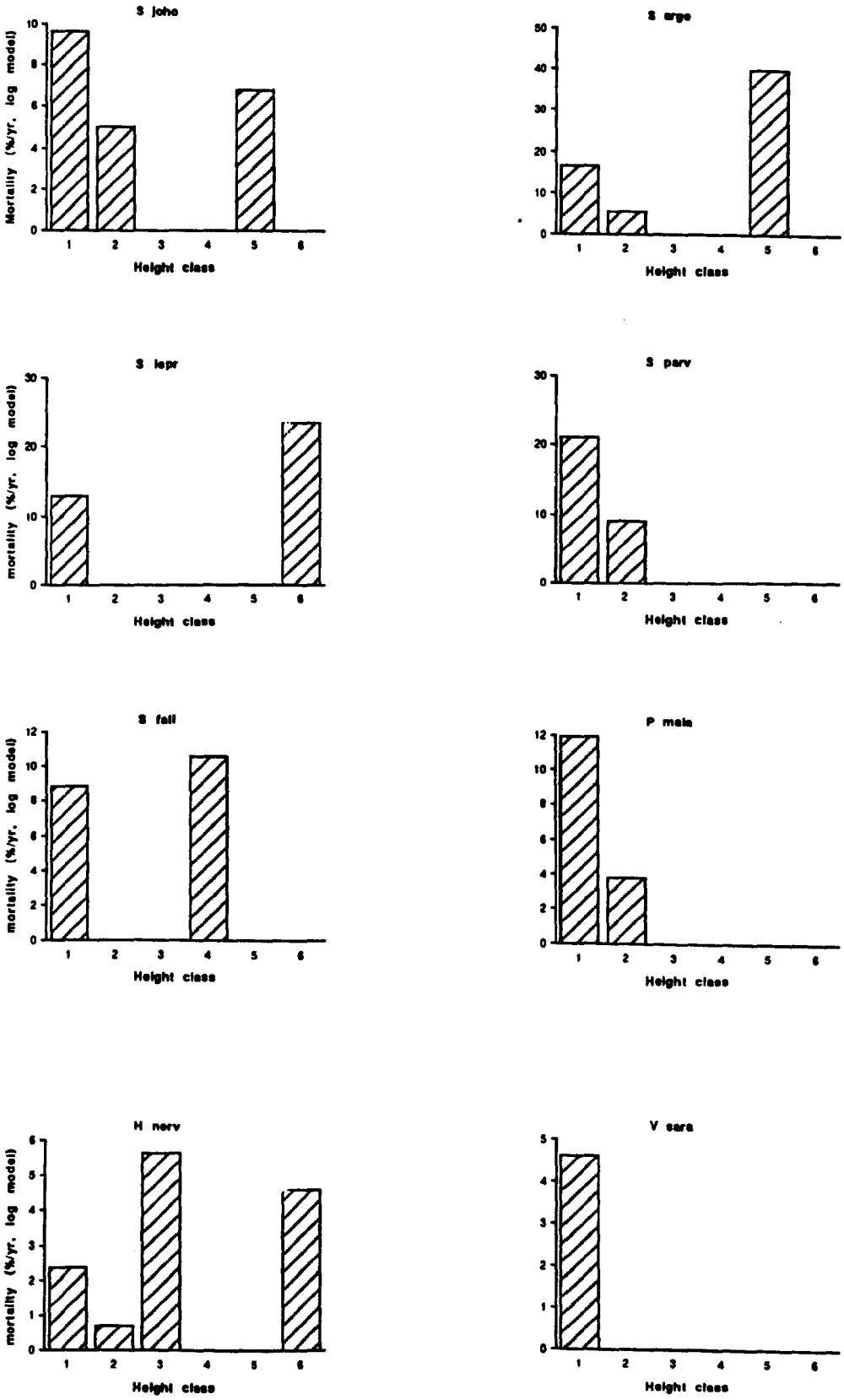


Figure 3.3

(b) Plot 2

The species with intermediate rates (5-10% yr^{-1}), *S. leprosula*, *S. parvifolia* and *S. pauciflora*, all showed a distinction between seedlings smaller and larger than 50 cm tall, with small seedlings experiencing much higher mortality than larger size classes. The contrast was greatest in *S. leprosula*, with mortality of 30% yr^{-1} seedlings less than 50 cm tall. In the species with low mortality rates (<5% yr^{-1}), *P. malaanonan* and *S. fallax*, mortality was similar in all size classes. The three LRMs and *S. fallax* all showed peaks in mortality in saplings 151-200 cm tall; in *P. malaanonan* a similar peak occurred at 201-300 cm.

In Plot 2, mortality was again generally highest in the smallest size classes in most species [Figure 3.3(b)]. Low numbers in some species mean that a single chance death will result in an apparently large mortality rate. The large peaks in mortality in *S. johorensis* and *S. argentifolia* (both in size class 151-200 cm) and *S. leprosula* (≥300 cm) were caused by the death of one out of fewer than ten individuals in the size class. Because of low numbers in some of the size classes, within-species comparisons of height class differences between the two plots are not statistically valid, though mortality patterns were broadly similar in most species. For example, in *S. parvifolia* mortality in both plots was much higher in seedlings smaller than 50 cm tall than in taller seedlings. *P. malaanonan* was an exception, and had clearly different profiles in each plot; in Plot 1 mortality was low (between 2 and 5%) in all five classes <300 cm, while in Plot 2, mortality was much higher (12%) in the smallest size class, rapidly decreasing to zero in saplings taller than 1 m.

Mortality of the 1985 cohort of *V. dulitensis* emphasises the high rates of very small seedlings (Figure 3.4). The seedlings were under 20 cm tall at first enumeration. Variation in mortality was great over a small range of initial heights. Over the first interval, mortality was very high, 76% yr^{-1}, dropping to 45% yr^{-1} over the second interval. Compared with seedlings of other species of the same size (≤20 cm tall), but unknown age, mortality of LRMs was very similar, 72% yr^{-1}, over the first interval, reducing to 24.2% yr^{-1} over the second interval. Mortality in DRMs of the same size was lower: 65% yr^{-1} and 16% yr^{-1} over the two intervals, while mortality in *P. malaanonan* was lower still (44% yr^{-1} and 10% yr^{-1}). Numbers of such small seedlings were low - in the LRMs and *P. malaanonan* only ten, and in the DRMs seven seedlings were smaller than 20 cm at the first enumeration.

In Plot 1, overall mortality rates in twelve height classes were compared for three species groupings (Figure 3.5). Mortality rates in the LRMs were consistently

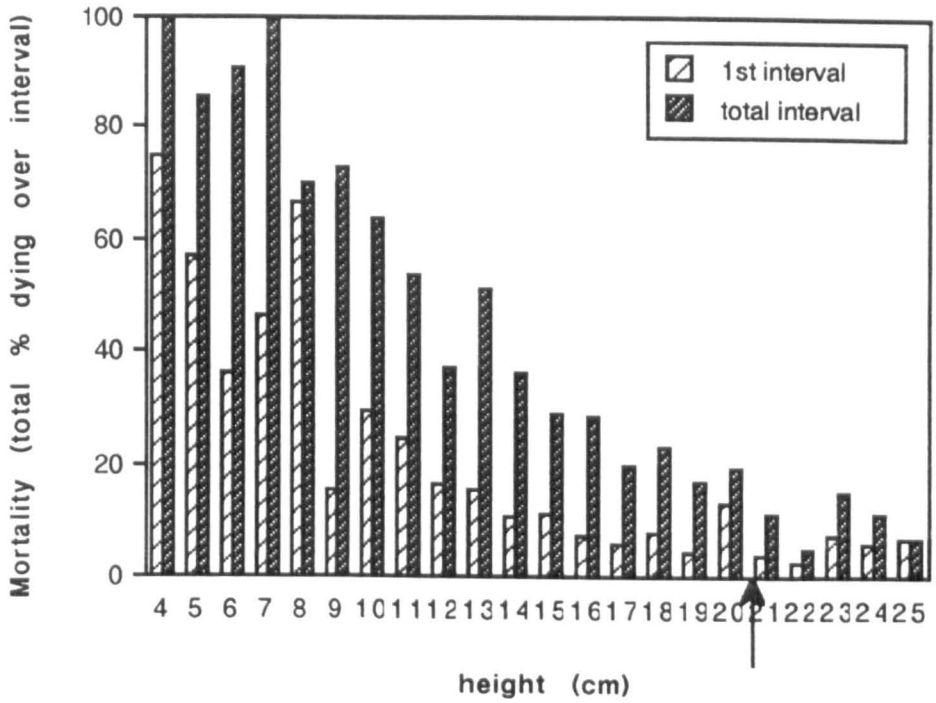


Figure 3.4 Size-related mortality in *Vatica dulitensis* seedlings 4-25 cm tall in Plot 1 during the first interval (19 weeks) and the total interval (91 weeks). Arrow marks the division between the 1985 cohort and older seedlings.

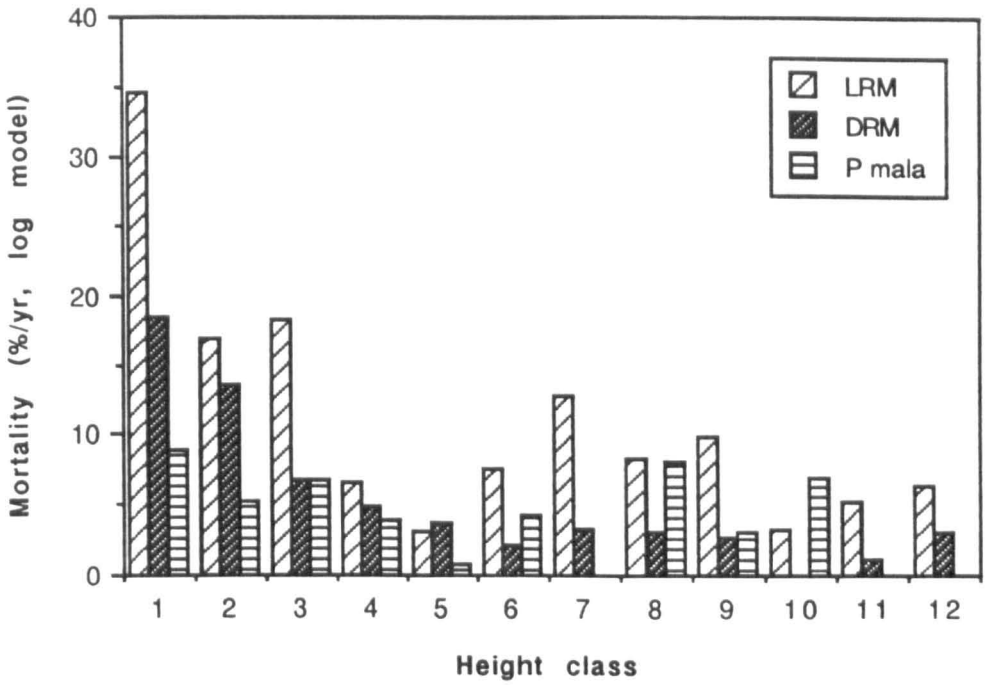


Figure 3.5 Comparison of size-related mortality rates of Light and Dark Red Merantis (LRM, DRM) and *Parashorea malaanonan* in twelve height classes in Plot 1. Height classes 1 to 10 are in 25 cm intervals; class 11, 251-300 cm; class 12, >300 cm.

higher than DRMs in all but one height class. In the two smallest height classes (≤50 cm), *P. malaanonan* had much lower mortality than either Meranti group.

3.4.3 Temporal variation

Mortality rates in the two intervals were compared as described in Section 3.3.4 for all species pooled in nine different height classes. There were significant differences in mortality between the two intervals in five of the nine height classes tested, but there was little evidence of consistent trends of changing mortality over time related to size. In the smallest seedlings (≤25 cm) and in saplings 250 to 300 cm tall, mortality was significantly lower in the second interval than in the first. Second interval mortality rates were higher in intermediate height classes: 76 to 100 cm and the two classes from 1.5 m to 2.5 m.

Mortality rates over the two intervals are compared for three species groupings, LRMs, DRMs and *P. malaanonan* in Figure 3.6. Clear trends were also lacking in the three species groupings: in no height class did all three groups show similar changes in mortality in the two intervals (Figure 3.6). For example, in seedlings 26 cm to 50 cm, LRM mortality was higher over the second interval, while that of DRMs and *P. malaanonan* was lower. In seedlings 1 to 1.5 m tall, second interval mortality was higher in DRMs but lower in *P. malaanonan*.

3.5 MORTALITY AND POPULATION DENSITY

One hypothesis to explain the high diversity of tree species in rain forest is the existence of compensatory mechanisms (Connell 1978, Connell *et al.* 1984). These are frequency- or density-dependent mechanisms which favour rare species at a site over common ones through increased rates of recruitment, survival and / or growth. Under this hypothesis, commoner species are predicted to have higher mortality rates than rare ones. This was tested by examining the relationship between seedling mortality rates and overall densities of both seedlings and trees in different species.

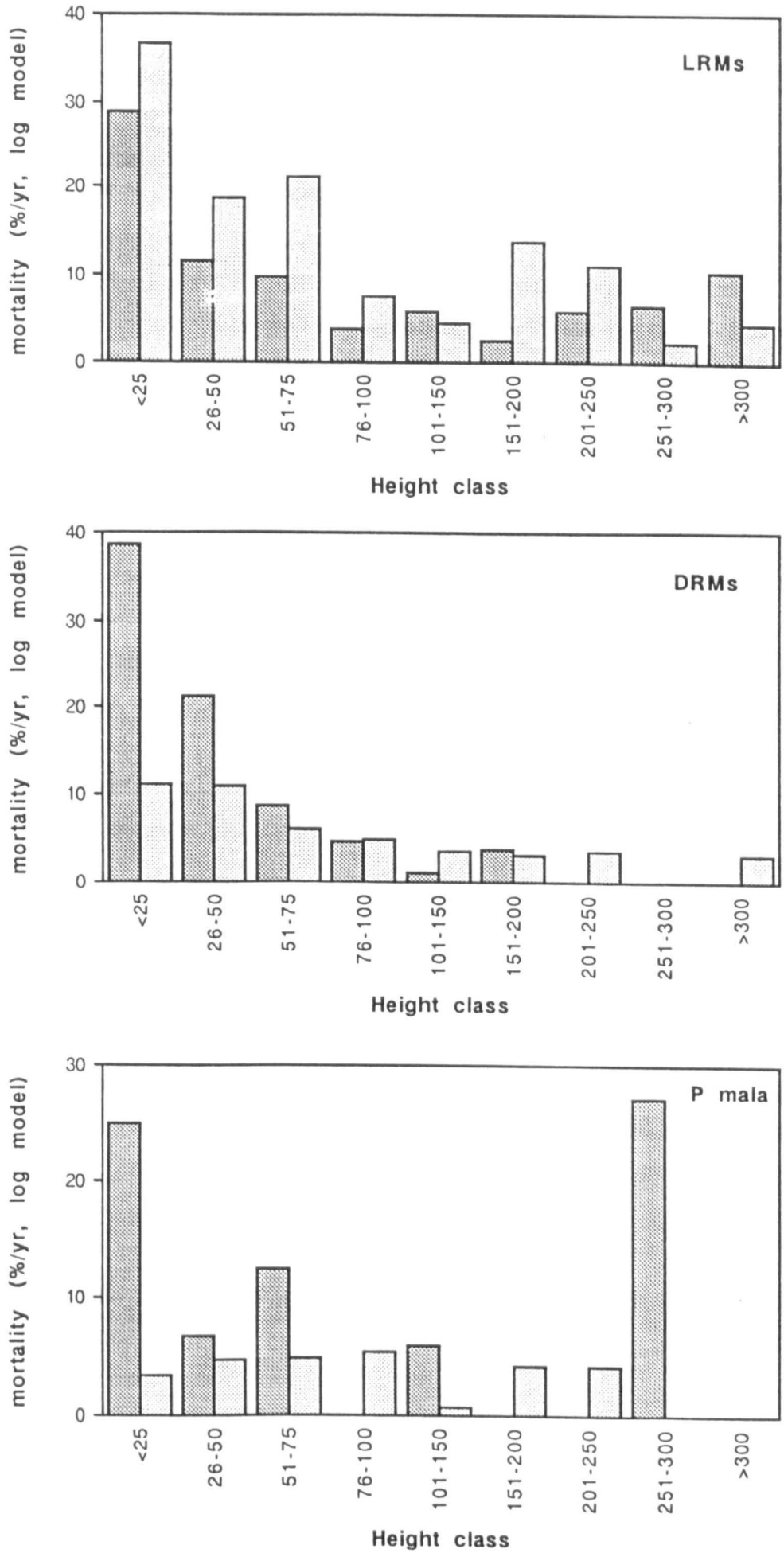


Figure 3.6 Comparison of first (dark shading) and second (light) interval mortality rates (% yr^{-1}, log model) in Plot 1 in nine height classes (cm) for three species groupings: Light and Dark Red Merantis (LRM, DRM), and *P. malaanonan* (P mala).

3.5.1 Mortality and seedling density

Mortality rate is plotted against log population density (ha^{-1}) of seedlings in Figure 3.7. Plot 1 species populations fall into three groups. The LRMs and *S. johorensis* had intermediate population densities and high rates of mortality. The three species with highest seedling population densities, *P. malaanonan* and the two DRMs, had intermediate mortality rates, while the remaining species fall into the third group, with low population sizes and low mortality rates.

Interpretation of this pattern is confounded by the fact that the species with intermediate abundances, the three LRMs, are taxonomically closely related with similar ecologies, and therefore more likely to have similar mortality rates. Similarly, the two DRMs both occur at high population densities. In Plot 2, the LRMs also had intermediate population densities and high rates of mortality relative to the other species.

A striking feature of Figure 3.7 is that within a species, in the plot with higher population density, mortality was also higher. This occurred in six of the eight species common to both plots in which seedlings died; an exception was *S. johorensis*, with higher mortality but lower population density in Plot 1. The six species were quite evenly split between plots in terms of which plot had the higher density and mortality: four were higher in Plot 2 and two in Plot 1.

3.5.2 Mortality and tree density

The relationship between seedling mortality rates and density of adult trees was investigated by regression analysis. Seedling mortality rate was the dependent variable regressed on the logarithm of number and basal area of conspecific adult trees within the two plots, so that each point represents one species. The independent variables were:

NTOT: ln(total number of trees ≥10 cm gbh)

N100: ln(total number of trees ≥100 cm gbh)

BATOT: ln(basal area of trees ≥10 cm gbh)

BA100: ln(basal area of trees ≥100 cm gbh).

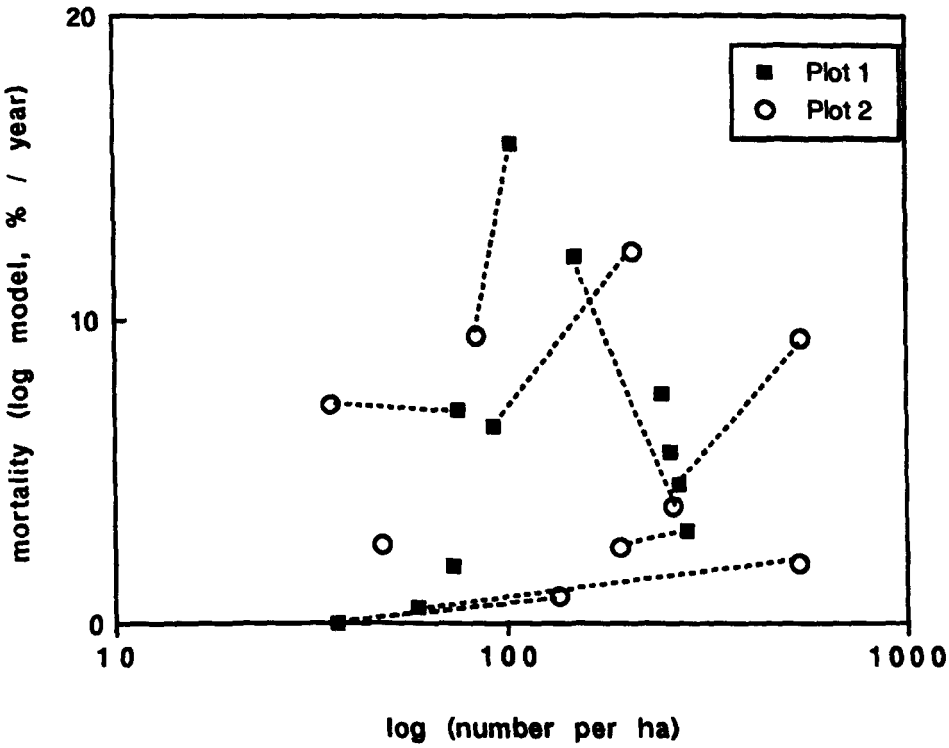


Figure 3.7 Relationship between seedling mortality rate and density of species in Plots 1 and 2. Dashed lines join points for the same species in the two plots.

In Plot 1, trees within the two hectare seedling study area were included. In Plot 2, trees were included if they lay within a 20 m border around the seedling study area (giving a total area of 1.2 ha). In *V. dulitensis*, mortality rate was used of seedlings over 20 cm tall (older than the 1985 cohort). In total, 10 species were included in Plot 1 and nine in Plot 2.

Regression equations are given in Table 3.3. Regressions of seedling mortality rate on both measures of basal area were significant in both plots. Seedling mortality was more closely related to basal area of large trees than to basal area of all trees. Relationship to total number of trees was not significant in either plot, but mortality was significantly related to the number of large (≥100 cm gbh) trees (which is highly correlated with basal area). Seedling mortality rate is plotted against the logarithm of basal area of large trees in Figure 3.8 for both plots.

In seven out of eight species common to both plots, seedling mortality was higher in the plot with the higher basal area of conspecific tree. The exception was *S. fallax*, in which mortality was slightly higher in Plot 1, while basal area was higher in Plot 2, though the rates were very similar in the two plots. As with the relationship to seedling density, the species were evenly split between plots, with four species having higher mortality and basal area in Plot 2 and three in Plot 1.

3.6 SPATIAL ASPECTS OF MORTALITY

3.6.1 Spatial variation in mortality within Plot 1

Mortality rates were calculated for 50 m x 50 m contiguous sub-plots in the seven major species in Plot 1, and for the two Meranti groups and all seven species pooled. Within each subplot, a χ^2 goodness-of-fit test was used to compare numbers dying in each subplot with the expected number calculated from the overall mortality rate and assuming equal mortality in each subplot. While the contiguous sub-plots are not independent observations, a χ^2 test was still considered appropriate.

Table 3.3 Equations for the regressions of seedling mortality rates (m, % yr^{-1}, log model) on number and basal area of conspecific adults. Independant variables are N100, BA100: the number and basal area of trees in each species ≥100 cm gbh; BATOT: total basal area of trees ≥10 cm gbh in each species. The regression of seedling mortality on NTOT, the total number of trees ≥10 cm gbh, was not significant in either plot.

	Regression equation	R^2(%)	P
Plot 1 (10 species)	m = 0.71 + 4.29 ln(N100)	58.9	**
	m = 5.41 + 2.83 ln(BATOT)	63.5	**
	m = 6.19 + 2.83 ln(BA100)	63.8	**
Plot 2 (9 species)	m = -0.34 + 3.84 ln(N100)	48.7	*
	m = 0.38 + 4.99 ln(BATOT)	45.0	*
	m = 0.75 + 4.91 ln(BA100)	46.7	*

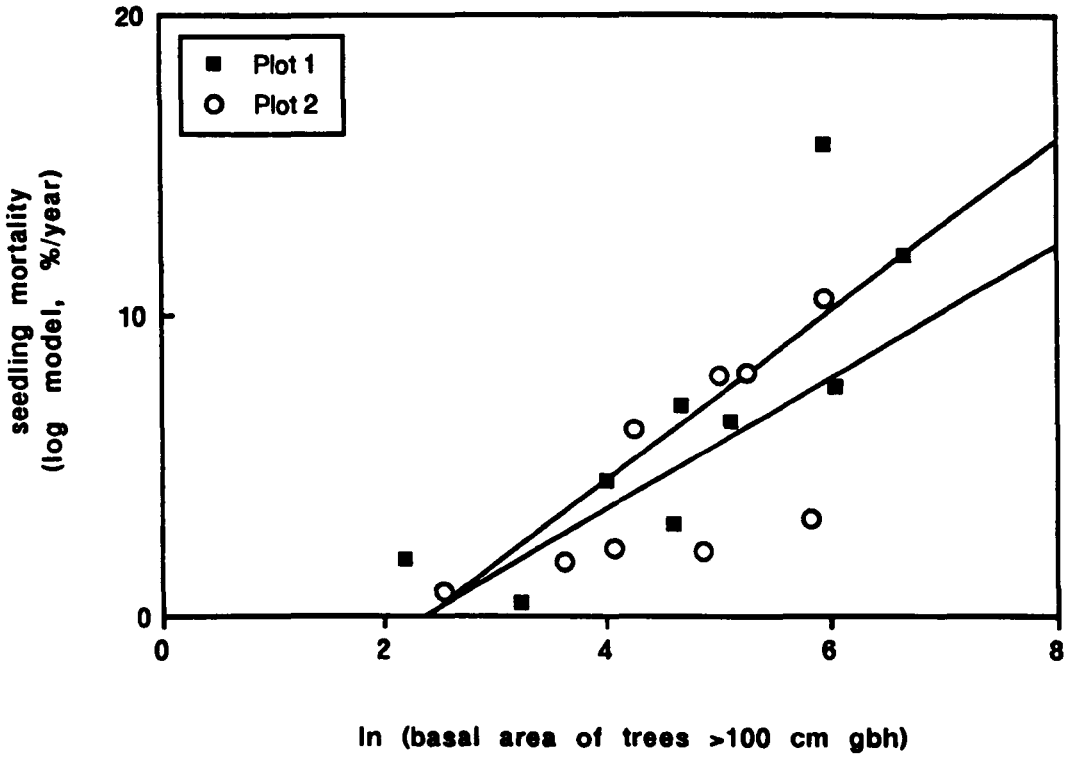


Figure 3.8 Relationship between seedling mortality rates and basal area of conspecific trees over 100 cm gbh in different species in Plots 1 and 2. Regressions are significant (see Table 3.3): Plot 1 (upper line), R^2=63.8%, P<0.01; Plot 2, R^2=46.7%, P<0.05.

3.6.1.1 Variation between species

Numbers of seedlings in a sub-plot could be low, so that apparently large differences in mortality were not significant because of small sample size. Mortality of all species pooled over the combined interval was significantly higher than expected in sub-plot C, and lower in sub-plots G and E. The range was from 3.6% (subplot G and E) to 10.5% (subplot C). Mortality in both DRMs and LRMs was very significantly higher than average in sub-plot C. DRM mortality was marginally below average in sub-plot H. Mortality ranged from 5% to 20% yr^{-1} in LRMs and from 1.2% to 12% yr^{-1} in DRMs.

Mortality within species varied quite widely between sub-plots (Table 3.4), but in the majority, rates did not differ significantly from expected. Only in three species/subplot combinations, all within the LRMs, were differences significant: in subplots C and D mortality rates of *S. argentifolia* and *S. leprosula* respectively were higher, while in subplot G, *S. argentifolia* had lower mortality than expected. Greatest variation in mortality over sub-plots was in *S. argentifolia*, ranging from 2.3% in subplot G to 29% yr^{-1} in subplot B.

3.6.1.2 Temporal variation

Within each species/sub-plot combination, second interval mortality was compared with first interval as previously described (Section 3.3.3). Mortality in the first and second intervals are given in Table 3.4 for each species/subplot combination.

Mortality differed significantly between the two intervals in six species/subplot combinations (Table 3.4). The largest difference in mortality was in *S. argentifolia* in subplot C, which increased from 8% to 33% yr^{-1} over the second interval. There was a parallel increase in mortality in two other species within this subplot, *S. johorensis* and *S. leprosula*, but these failed to reach significance. Mortality in *P. malaanonan* and *S. parvifolia* actually decreased significantly in the same subplot. This subplot alone accounted for three of the six significant differences, two decreases and an increase. The high mortality rates experienced in some subplots were not sustained: no species suffered consistently high mortality over both intervals in any

Table 3.4 Variation in mortality rate (% yr^{-1}, log model) in eight 50x50m sub-plots in first, second and total intervals in Plot 1. P^1: * indicates sub-plot mortality (total) significantly different ($P<0.05$) from overall mortality in each species, P^2: * indicates significant difference ($P<0.05$) between first and second interval mortality rate, see text for details.

sub-plot	Species	N	dead	mortality rate 1st	mortality rate 2nd	mortality rate total	P^1	P^2
A	S joho	51	8	3.81	10.75	8.87		**
	S arge	26	6	15.42	12.99	13.64		
	S lepr	7	2	64.46	0.00	17.50		
	S parv	28	4	0.00	10.99	8.02		
	S fall	3	0	0.00	9.99	0.00		
	S pauc	113	14	6.90	6.79	6.82		
	P mala	96	6	2.02	3.85	3.36		
B	S joho	23	5	8.53	14.31	12.75		
	S arge	7	3	0.00	39.86	29.10		
	S lepr	11	0	0.00	0.00	0.00		
	S parv	0	-	-	-	-		
	S fall	19	3	10.37	8.40	8.94		
	S pauc	25	5	33.43	3.48	11.60		*
	P mala	111	13	8.93	5.59	6.49		
C	S joho	14	5	13.87	26.47	22.98		
	S arge	71	25	8.16	32.95	26.12	*	***
	S lepr	13	1	0.00	5.77	4.18		
	S parv	17	2	24.00	0.00	6.55		*
	S fall	10	0	0.00	0.00	0.00		
	S pauc	233	41	8.32	10.78	10.11		
	P mala	154	16	11.48	3.57	5.74		**
D	S joho	28	8	0.00	24.30	18.04		
	S arge	17	4	12.21	14.98	14.24		
	S lepr	16	6	12.26	29.28	24.59	*	
	S parv	23	4	17.66	7.22	10.05		
	S fall	6	0	0.00	0.00	0.00		
	S pauc	35	1	5.77	0.00	1.54		
	P mala	72	3	0.00	3.07	2.24		

Table 3.4 cont.

sub-plot	Species	N	dead	mortality rate 1st	2nd	total	P1	P2
E	S joho	27	5	8.85	12.07	11.31		
	S arge	6	0	0.00	0.00	0.00		
	S lepr	2	0	0.00	0.00	0.00		
	S parv	7	0	0.00	0.00	0.00		
	S fall	118	7	6.05	2.56	3.38		
	S pauc	62	5	11.36	2.49	4.62		*
	P mala	62	1	0.00	1.17	0.90		
F	S joho	94	19	15.56	11.54	12.49		
	S arge	40	7	12.14	10.19	10.65		
	S lepr	83	7	0.00	6.36	4.87		
	S parv	26	2	9.37	2.95	4.44		
	S fall	32	2	0.00	4.66	3.58		
	S pauc	14	0	0.00	0.00	0.00		
	P mala	40	3	5.92	3.80	4.30		
G	S joho	15	3	0.00	16.28	12.53		
	S arge	25	1	0.00	2.98	2.30	*	
	S lepr	3	0	0.00	0.00	0.00		
	S parv	17	1	0.00	4.43	3.41		
	S fall	301	18	3.27	3.52	3.46		
	S pauc	7	0	0.00	0.00	0.00		
	P mala	2	0	0.00	0.00	0.00		
H	S joho	46	6	5.44	8.51	7.82		
	S arge	13	3	19.82	13.20	14.71		
	S lepr	14	2	0.00	11.13	8.63		
	S parv	48	4	0.00	6.29	4.87		
	S fall	93	2	0.00	1.58	1.22		
	S pauc	1	0	0.00	0.00	0.00		
	P mala	4	0	0.00	0.00	0.00		

subplot. Otherwise, there is little serial correlation between mortality rates, despite lack of significant differences between intervals.

Looking at the two Meranti groups (Figure 3.9), there were significant differences in mortality between intervals in five combinations. In three, all in the LRMs, mortality was significantly higher in the second interval, while the remaining two were decreases, both in the DRMs. Overall mortality (seven major species pooled) was significantly lower over the second interval in subplots E and H, both dominated by DRMs. Mortality increased in subplot D, an area with a large proportion of LRMs. In *P. malaanonan*, there were no significant differences between intervals in any subplot.

3.6.1.3 Mortality and seedling density

Mortality rates are plotted against the logarithm of species population density in each sub-plot for three species groupings (Fig 3.10). It is important to note when interpreting the observed patterns that the points are not independent: there is likely to be greater correlation of mortality rates, and population densities, as well as environmental conditions in adjacent sub-plots than in more distant sub-plots.

Bearing this in mind, there is evidence of an increase in mortality with increasing density in *P. malaanonan*, which was the most abundant and widespread seedling species in the plot. There is also a suggestion of a similar relationship in the Light Red Merantis, but the sub-plot with highest population density had an intermediate rate of mortality. In the Dark Red Merantis, highest mortality occurred in the sub-plot with the lowest population density.

3.6.2 Mortality and proximity of large conspecific trees.

Mortality rates were compared for seedlings in two categories: those growing beneath conspecific versus heterospecific large dipterocarp trees. A seedling was defined as beneath a large tree in this analysis if it was 10 m or less from the centre of the tree stem. Seedlings which lay within 10 m of two large trees were assigned to the nearer tree. A further comparison was made with seedlings growing more

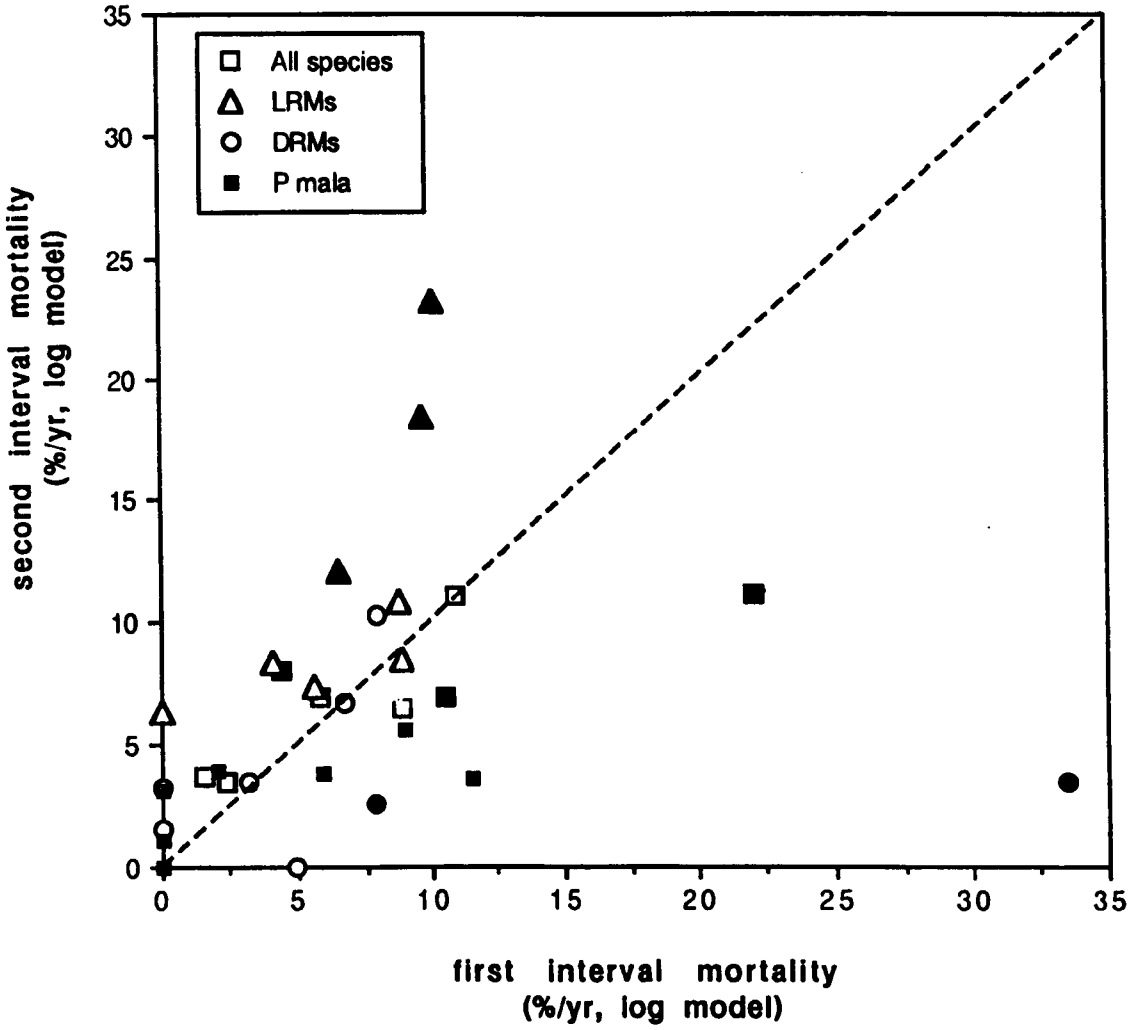


Figure 3.9 Comparison of first and second interval mortality rates (%/yr, log model) in three species groups (LRM, DRM: Light and Dark Red Merantis, and *Parashorea malaanonan*) and in all species pooled, within eight 50x50 m subplots in Plot 1. Diagonal line indicates equal mortality in both intervals. Filled symbols indicate significant difference in mortality rate betwen intervals ($P<0.05$, see text for details).

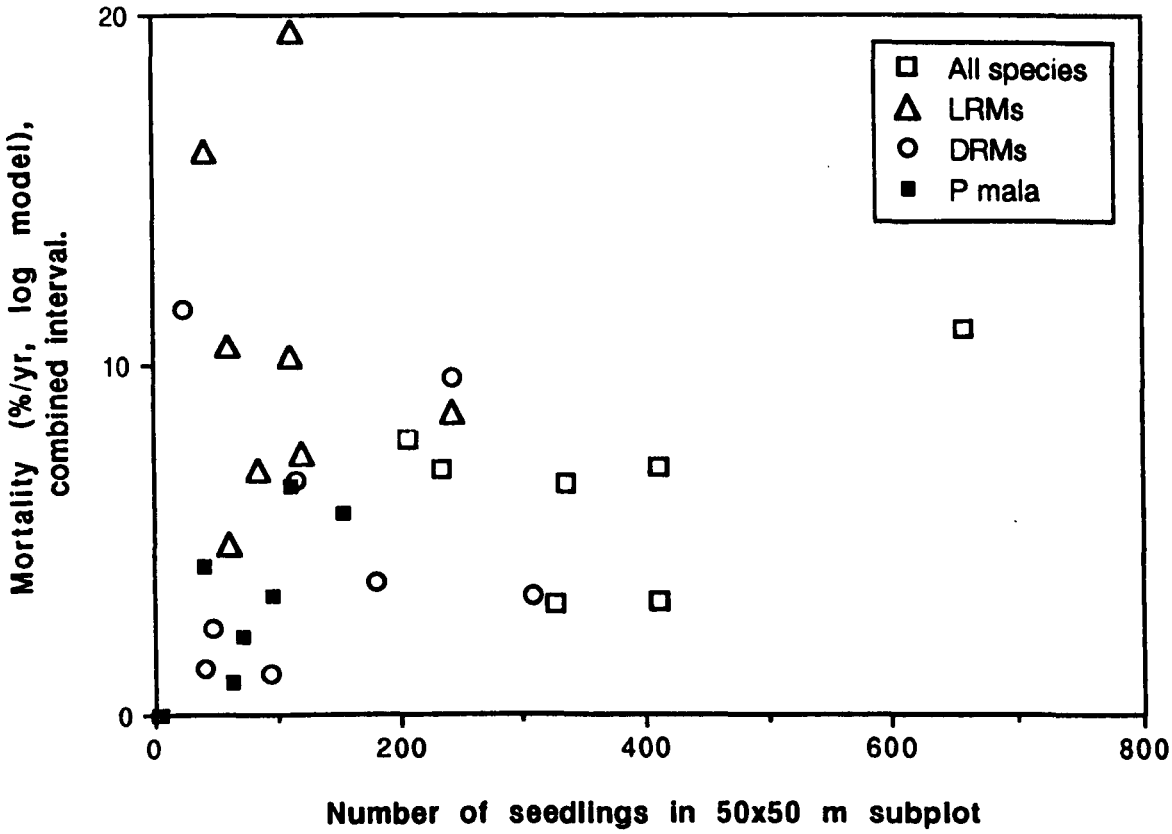


Figure 3.10 Mortality (%/yr, log model) in three species groups (LRM, DRM: Light and Dark Red Merantis, and *P. malaanonan*) and in all species pooled in relation to density within eight 50x50 m subplots in Plot 1.

than 10 m from any large dipterocarp. Six species in Plot 1 had sufficient numbers of large trees and dead seedlings in each category to test. In *P. malaanonan*, only one seedling grew beneath a conspecific tree, and it survived.

3.6.2.1 Results

Numbers alive and dead at the third enumeration and mortality rates, defined here as the percentage of seedlings dying over the entire enumeration period, are given in Table 3.5.

In all six species pooled, mortality was almost double in seedlings growing beneath a large conspecific tree compared with beneath a heterospecific tree (χ^2=18.7, df=1, P<.001). In individual species, seedlings growing beneath conspecific trees had higher mortality than those growing beneath heterospecific trees in all six species. Differences in mortality were statistically significant in two species, *S. johorensis* and *S. pauciflora*, in which mortality rates beneath a conspecific tree were respectively three times and twice the rate below a heterospecific tree.

Mortality in seedlings growing more than 10 m from any large dipterocarp was intermediate between the other groups. Lowest mortality (9%) was in seedlings growing beneath a heterospecific dipterocarp. In five out of seven species (*P. malaanonan* included in this comparison), mortality in seedlings beneath a heterospecific tree was lower than in seedlings more than 10 m from any large dipterocarp. In two species, *S. johorensis* and *S. parvifolia*, mortality beneath a conspecific tree was similar to that of seedlings more than 10 m from any dipterocarp and more than twice the mortality rate of seedlings beneath a heterospecific dipterocarp. In contrast, seedlings of two species, *S. fallax* and *P. malaanonan* experienced highest mortality when they grew more than 10 m from any large dipterocarp. There was no clear relationship between category with the highest mortality and taxonomic grouping.

3.6.3 Reasons for increased mortality below a conspecific tree

To establish whether the observed effects on mortality are really conspecific effects, perhaps through the predator-attraction effect of a large conspecific tree

Table 3.5 Comparison of mortality (toal % dying between the first and final enumeration) between seedlings growing beneath conspecific versus heterospecific large (≥100 cm dbh) dipterocarp trees and seedlings growing > 10m from any large dipterocarp in Plot 1. *P* value is from a χ^2 test of 2x2 contingency table comparing mortality beneath conspecific versus heterospecific trees.

	beneath conspecific			beneath heterospecific			> 10m from any dipterocarp			
	numbers			numbers			numbers			
Species	dead	live	% dead	dead	live	% dead	dead	live	% dead	*P*
S joho	23	81	22.1	5	55	8.3	23	131	22.0	*
S arge	3	3	50.0	31	104	23.0	23	81	22.1	N.S.
S lepr	2	2	50.0	9	84	9.7	7	52	11.9	N.S.
S parv	1	7	12.5	10	85	10.5	13	93	12.3	N.S.
S fall	5	90	5.3	14	274	4.9	17	224	7.1	N.S.
S pauc	29	120	19.5	9	112	7.4	34	250	12.0	*
P mala	0	1	0.0	18	262	6.4	30	278	9.7	-
Total	63	304	17.2	96	976	9.0	161	1109	12.7	***

(Connell 1971), other, potentially correlated, factors must be separated. Conspecific trees could be (1) larger, or (2) closer to their seedlings than heterospecific trees. Seedlings growing beneath a conspecific tree could be (3) at higher density or be (4) smaller on average than seedlings growing elsewhere, perhaps because of poor seed dispersal. These factors could vary between species as well as between categories within the same species.

3.6.3.1 Size of tree

If the cut-off girth for inclusion of large trees is lowered to 60 m gbh, the trends in mortality were similar, but the magnitude of differences was reduced. Overall, mortality was still greatest in seedlings beneath a conspecific tree, but reduced to 14.2% compared to 17.2% beneath trees over 100 cm gbh. Lowest mortality was again in seedlings beneath a heterospecific dipterocarp, but increased from 9.0% to 11.1%. In the two species with significant differences in mortality between seedlings beneath conspecific versus heterospecific trees, *S. johorensis* and *S. pauciflora*, mean size of large (≥100 cm gbh) trees was among the highest. Additionally, these two species have the highest basal area of trees in the 2 ha study area.

3.6.3.2 Distance

Distance frequency distributions were compared between seedlings growing below conspecific versus heterospecific trees to test whether conspecific trees were closer to seedlings than heterospecific trees.

For the six species pooled, distance distributions were similar (Kolmogorov-Smirnov test, $P>0.05$) in the two categories. In individual species, *S. parvifolia* seedlings were significantly closer to conspecific trees than to heterospecific trees, but there was no difference in mortality between these categories. In the two species in which mortality did differ between categories, there was no difference in distance distributions in *S. pauciflora*, while in *S. johorensis*, difference approached significance ($P=0.057$), but seedlings were on average further from conspecific trees than heterospecific trees (mean distances were 6.8 m beneath conspecific trees and 6.1 m beneath heterospecific trees). This would be expected to act against the currently observed patterns of mortality, but may be evidence of strong differential mortality in the past.

3.6.3.3 Density

The two species with significantly higher mortality under conspecific trees both had a relatively high density of conspecific seedlings growing below large trees. In *S. johorensis*, mean density of seedlings within 10 m of large trees was 259 ha^{-1}, and in *S. pauciflora*, 913 ha^{-1}. In two other species, *S. fallax* and *H. nervosa*, seedling density below large trees exceeded 200 ha^{-1}, but mortality rates were among the lowest. These results suggest that for some species, though not all, density of conspecific seedlings may be one factor reinforcing the deleterious effects of proximity to a conspecific large tree.

3.6.3.4 Differences in seedling size

In species with a high density of conspecific seedlings beneath large trees (a consequence of poor seed dispersal), a higher proportion of small seedlings might be expected beneath the tree than would be found at greater distances from large trees. Since small seedlings often had higher mortality rates (Section 3.4.2), mortality beneath a conspecific adult may be higher for this reason, rather than because of any effect of the conspecific tree.

Differences in height frequency distributions between seedlings growing below a conspecific (N=367) versus heterospecific (N=789) large tree were tested with a χ^2 test of independence. There was a significantly greater proportion of small seedlings below conspecific large trees: 57% were less than 1 m tall compared to 44% beneath heterospecific trees (χ^2=15.73, df=1, P<0.01). A significantly smaller proportion of seedlings exceeded 3 m tall beneath conspecific trees, 6%, versus heterospecific trees, 12% (χ^2=10.02, df=1, P<0.01).

In individual species, differences in height distribution approached significance in *S. argentifolia* (Kolmogorov-Smirnov test, P=0.063) and were highly significant in *S. pauciflora* (Kolmogorov-Smirnov test, P<0.001). In *S. argentifolia*, only six saplings grew beneath large trees of the same species, and all were less than 1 m tall, compared with 62% of those under trees of other species. In *S. pauciflora*, differences in height distributions were highly significant (Kolmogorov-Smirnov test, P<0.001). Beneath conspecific large trees, 79% of seedlings were smaller than 1 m tall, and only 2.7% exceeded 2.5 m tall, compared with 62% and 21% respectively for seedlings beneath heterospecific trees. But this large difference in height structure does not

alone account for the observed differences in mortality in the two categories. If expected mortality is calculated for each category using the observed height-class mortality rates of all *S. pauciflora* seedlings, and weighting for the differences in height-class frequency, some, but not all of the difference in mortality can be accounted for. Expected mortality was calculated in this way to be 15.4% for seedlings beneath conspecific trees and 10.8% beneath heterospecific trees, compared to the observed mortality of 19.5% and 7.4% respectively.

Again, it is difficult to separate cause and effect: the smaller proportions of large saplings observed beneath conspecific trees may be the result of past differential mortality rather than the cause of currently observed trends. The seedlings are survivors of cohorts at least four years old, and many will be older.

3.7 DISCUSSION

Mortality due to litterfall

The importance of tree and branch falls in seedling mortality regimes has been noted by other workers. In the unstable environment of tree-fall gaps, Nunez-Farfan & Dirzo (1988) conclude that litter-fall is an important cause of death in Mexican rain forest seedlings. In closed forest, Aide (1987) recorded cause of death in a study of liane seedlings, *Connarus turczaninowii*, from 30-300 cm height. In two consecutive years, tree and limb-falls caused 22.2% and 47.6% of deaths. Branch and tree-fall caused 50% of the annual mortality in juvenile *Pentaclethra macroloba* in Costa Rica (Hartshorn 1972, in Aide 1987). Also in Costa Rica, Clark & Clark (1987) followed one cohort of *Dipteryx panamensis* seedlings over 52 months and recorded litterfall as responsible for a minimum of 16% of deaths. In larger individuals, 1-10 cm dbh, litterfall caused 38% of deaths in Venezuelan tierra firme forest (Uhl 1982).

In central American palms, Sarukhàn (1978) suggests that limb and tree-falls kill a major proportion of juvenile and sub-reproductive stages of *Astrocaryum mexicanum*, while litter-fall caused one third of deaths over seven years in mature individuals of the same species (Piñero *et al.* 1984). Litter-fall killed 18% of *Welfia georgii* seedlings over nine months (Vandermeer 1977). Large-leaved palms are

themselves an important source of litter, potentially damaging to surrounding plants. Seedlings are often killed by falling palm fronds in Malaysia (Dransfield 1978), Costa Rica (Vandermeer 1977) and Panama (Aide 1987).

In a study specifically designed to measure the importance of physical damage, Clark & Clark (1989) used artificial seedlings (made of wire and plastic straws) set out along 500 m transects in La Selva, Costa Rica, and surveyed monthly. They found that 19% were damaged (bent to the ground, flattened or buried) by tree or branch falls in one year.

In Malaysian rain forests, Burgess (unpubl. in Whitmore 1984) studied seedling establishment after the heavy fruiting in 1968, and found that much of the mortality was caused by "falling twigs". Becker & Wong (1985) studied mortality in a population of 127 seedlings of *Aglaia* sp. on a one ha plot in Pasoh, West Malaysia., and found circumstantial evidence that a tree-fall killed only one or two of the 38 seedlings which died during the four-year study period.

There is great variation in mortality rates in the above studies. Size may be one factor in the variation. Small seedlings may be less likely to survive litter-fall damage than larger individuals (Aide 1987), although it can continue to be an important cause of mortality (eg. Piñero *et al.* 1984). Larger seedlings may be only partially buried by litter that could completely cover a smaller seedling. The ability to re-sprout after burial is also likely to be size-related: smaller seedlings with smaller root systems may have insufficient nutrient reserves to permit re-sprouting if most of the leaves have been lost. (Many seedlings in the present study showed scars or signs of re-sprouting following stem damage). There were few differences between size classes in mortality due to litter-fall, but litter-fall mortality may have been underestimated more in smaller size classes because small seedlings were more likely to have decomposed between enumerations.

Slow-growing seedlings may have a higher probability of being damaged by litter-fall (Aide 1987) because they remain smaller for longer. Dipterocarp species which can remain suppressed for long periods, forming a seedling bank, may be more vulnerable to litter-fall damage because of this. *P. malaanonan* for example can persist for years at around 30 cm height (Meijer & Wood 1964). The rate of litter-fall mortality was significantly higher in *P. malaanonan* at Danum (19.3%). *V. dulitensis* was another species with a high proportion of small seedlings (10-20 cm tall), many of which survived for 22 months with the original pair of true leaves and were

particularly vulnerable to burial by even small debris such as leaves and small branches. The rate of litter-fall mortality in *V. dulitensis* was similar to the overall rate, but these small seedlings decomposed quickly: 57% had disappeared between the second and third enumerations, many of which could have been killed by falling litter. Mortality attributed to falling debris is therefore likely to be considerably underestimated in this species.

Occasionally, seedlings were found uprooted by mammals, probably bearded pigs (*Sus barbatus*), outside the study areas. Damage and herbivory by mammals is important in mortality regimes for seedlings in temperate forests (eg. Sork 1987, Myster & McCarthy 1989) but grazing by vertebrate herbivores was never observed or detected, and seems to be negligible in dipterocarp seedlings in Danum. Damage caused by invertebrates to leaves and stems was ubiquitous, but no deaths could be attributed and complete defoliation was never observed.

Variation between species

It is useful to discuss variation in mortality rates in terms of mortality of species, or groups of closely related species, relative to others. The discussion will concentrate on this aspect of species mortality rates in the Danum plots, and comparisons will be made with other studies, mostly within Sabah. Whitmore (1984) has cautioned that comparing dipterocarp seedling mortality rates in different areas can be "very misleading". Many factors operating on a local level can vary greatly between studies in different areas and years, such as age of seedlings, local seedling density, slope, climatic variables, and soil type and nutrients. These factors are not always described for each study.

Fox's (1972) study of natural regeneration of dipterocarp forest in Sabah also found considerable variation in mortality between species. Seedlings of two Light Red Merantis, *S. parvifolia* and *S. argentifolia*, had similar mortality patterns, with large numbers of seedlings appearing after a fruit fall, but most dying over the next few years. *S. johorensis* seedlings survived longer and population size fluctuated less. In Plot 2, behaviour of these species is similar to that reported by Fox: all three Light Red Merantis present had higher mortality than *S. johorensis*. In Plot 1, mortality of *S. johorensis* was higher than in two of the Light Red Merantis, *S. leprosula* and *S. parvifolia*, but lower than in *S. argentifolia*.

In eastern Sabah, Liew & Wong (1973) found that seedling mortality of *S. parvifolia* was higher than *P. tomentella*, closely related to *P. malaanonan*. In the present study, mortality of *S. parvifolia* was higher than *P. malaanonan* in both plots. In Plot 1, mortality in both species decreased with time, and, while mortality in *S. parvifolia* remained higher than in *P. malaanonan* in both intervals, mortality was higher in *P. malaanonan* in the first interval (6.7% yr^{-1}) than in *S. parvifolia* in the second (5.9% yr^{-1}). *P. malaanonan* mortality in Plot 2 was higher than overall *S. parvifolia* mortality in Plot 1. Mortality rates for these two species varied in space and time, but where the two species were growing together, *S. parvifolia* had consistently higher mortality than *P. malaanonan*. Although the actual mortality rates may vary, this suggests there are inherent differences in mortality rates between species.

Liew & Wong (1973) also found that mortality of *S. parvifolia* was higher than in the other three *Shorea* species in their study, each representing a different Section of the genus: *S. superba*, a Selangan Batu, (Sect. *Shorea*). *S. ovalis*, a Dark Red Meranti (Sect. *Ovalis*) and *S. gibbosa*, a Yellow Meranti (Sect. *Richetoides*). There were no Selangan Batu or Yellow Meranti species present as in the Danum seedling study areas, but Dark Red Merantis were present. In both plots, *S. parvifolia* had higher mortality than one of the Dark Red Merantis, *S. fallax*, but in Plot 1, *S. parvifolia* mortality was lower than in the other DRM, *S. pauciflora*. In another study comparing species in different groups, in Peninsular Malaysia, populations of *S. leprosula*, (Light Red Meranti), had higher mortality rates than *S. maxwelliana*, a Selangan Batu (Sect. *Shorea*) (Becker 1983). In Danum Valley, Brown (1990) found that mortality rates in three species were ranked (highest to lowest) *P. malaanonan* > *S. johorensis* > *H. nervosa*, the same order as in Plot 2 in the present study; in Plot 1, mortality of *S. johorensis* was higher than that of *P. malaanonan*.

Turning to actual rates, and bearing in mind the points mentioned above, it is also worth noting that most studies have followed single seedling cohorts from recruitment, whereas the Danum seedling populations are multiple overlapping cohorts and include juveniles up to 10 cm gbh. Liew & Wong's (1973) seedling populations were recruited after a heavy fruit fall in 1967. Annual percentage mortality rate for *S. parvifolia* was 49% yr^{-1} in the fifth year (from Fig 4, Liew & Wong 1973). In the Danum plots, mortality of *S. parvifolia* (annual percentage) was 6.1% yr^{-1} and 11.0% yr^{-1} in Plot 1 and 2 respectively, lower than those reported by Liew & Wong (1973). These rates give an estimated half-life for 4 to 10 year-old *S. parvifolia*

seedlings of 3.5 years, compared with eight to ten years in the present study for seedlings of unknown age structure, but certainly including seedlings older than five years. Time since the last recruitment event in Danum is unknown. Assuming that the smallest seedlings are also the youngest, we can compare the observed mortality for the smallest size class (<50 cm) in *S. parvifolia* (16.5%-17.7%) (Figure 3.2) with the results of Liew & Wong (1973). Again, mortality of even the smallest seedlings in the Danum populations is lower.

In Peninsular Malaysia, mortality of *S. leprosula* censussed from the age of 21 months was around 30% yr^{-1} calculated over a 2-year period and including accidental deaths (Becker 1983). This is much higher than rates observed in the Danum populations of *S. leprosula*: 6.5% yr^{-1} in Plot 2 and 6.6% yr^{-1} overall rate in Plot 1. Mortality in the smallest size class of *S. leprosula* was 23.1% yr^{-1} and 11.6% yr^{-1} in Plots 1 and 2 respectively, again lower than Becker's value for seedlings less than four years old. Both the studies quoted above censussed single cohorts, within five years of recruitment, so meaningful comparison of mortality rates is difficult.

Other studies report lower mortality rates for dipterocarp seedlings. Liew & Wong (1973) quote survival of 96% for the first year after recruitment in Madai Forest, a Reserve on rich volcanic soils. However, no details of population size, density or species composition are given. At Sepilok Forest Reserve, another floristically rich forest on sandstone ridge type soils, mortality rates of Red Merantis reported by Fox (1972) are similar to the present study, varying between 10% and 20% in most years for cohorts 3 - 10 years old.

Mortality and size

Mortality of juvenile plants is often size-dependent (Cook 1979). Other studies of tropical tree seedlings have shown that even small size differences influence the chance of survival. In *Shorea robusta*, a gregarious species from the Himalayan foot-hills, mortality was higher in small seedlings, less than 10 cm tall, than in the 11-20 cm and 21-30 cm classes in old growth forest (Rao & Singh 1985). Clark & Clark (1987) found that survival over 52 months in seedlings of *Dipteryx panamensis*, an emergent tree, in Costa Rica was significantly correlated with stem diameter at 7 months, which ranged from 2.2 mm to 4.4 mm. In seedlings <50 cm height of an

Aglaia species in Pasoh, Malaysia, those that died were significantly smaller than survivors (Becker & Wong 1985).

In the Danum plots, mortality of the 1985 cohort of *V. dulitensis* was very strongly size-related. In three species in Plot 1, there was a clear peak in mortality in the smallest seedlings (≤50 cm), while mortality in the larger size classes was similar. In a further two species (*S. fallax, P. malaanonan*), mortality was low and constant throughout the size range. Welden *et al.* (1991) found that survival was high and constant in size classes over 1 cm dbh in shade tolerant canopy species at La Selva, Costa Rica. In the present study, the species with the greatest contrast between mortality in the smallest versus larger seedlings were the light-demanding emergent species.

Temporal and spatial variation in mortality

The data on changes in mortality over time are limited; with mortality estimates for only two intervals, no general trends can be discerned. Mortality rates can only be compared between two intervals in Plot 1. Mortality was significantly lower over the second interval than over the first in two species in the present study, and significantly greater in three species.

Decreasing mortality with time (age) is often observed in cohorts of tree seedlings (Cook 1979). Increasing mortality is less common. An explanation may lie in the seasonality of rainfall (see Chapter 1.4.2). The first enumeration (July to September 1986) began two to three months after the 1986 dry season, and the second enumeration (February 1987) was done towards the end of the next rainy season; the intervening period had medium rainfall. The dry season of 1987 was from April to June, and the 1988 dry season from mid-March to late May. During the first interval, therefore, there was no dry period, whereas in the second interval, seedling populations experienced two dry seasons, periods of potential drought stress, when mortality rates may have been higher. Mortality rates were significantly higher over the second interval in *S. johorensis*, *S. argentifolia* and *S. leprosula*, all fast-growing species, which may be more susceptible to water stress.

Mortality rates in two *Shorea* species, *S. maxwelliana* and *S. leprosula* varied with time (Becker 1983): in some populations, mortality rate was constant over time, while

in others, mortality decreased. Mortality in seedling *Tachigalia versicolor*, a monocarpic canopy tree studied on Barro Colorado Island, Panama decreased with age, even during the dry season (Kitajima & Augspurger 1989).

Spatial and temporal fluctuations in mortality rates were greatest in the Light Red Merantis, especially in *S. argentifolia*, which had the highest overall rate. Mortality in this species appeared to be confined to 'hot-spots' which did not persist over time. Species did not always react in the same way within the same local area and time interval. This was particularly notable in subplot C, in which a large increase in mortality in *S. argentifolia* was accompanied by a decrease in mortality in two other species. Subplot C contained a small recent canopy gap caused by a branch fall. Debris was suspended over a small patch of *S. argentifolia* seedlings, greatly increasing shading, but without causing physical damage, and most seedlings in the patch died. The increase in light in the rest of the subplot may have enhanced survival of other seedlings. This illustrates the very small spatial scale of some seedling mortality processes, and it is likely that factors influencing mortality operate on time scales too short to have been detected by the present study, and on smaller spatial scales than the 50 m x 50 m scale tested.

Density-dependent mortality

On the scale of the seedling study areas, there was evidence for the existence of compensatory mechanisms, through density-dependent mortality. In both plots, seedling mortality rates were higher in species with high basal area of trees, and lower in less abundant species. This relationship seemed to hold both between species and within: mortality within a species was almost always higher in the plot with higher density. This applied to density of both seedlings (Figure 3.7) and trees (Figure 3.8). Evidence for the mechanism was sought on a more local scale: is proximity to a large conspecific tree deleterious for a seedling? Mortality was found to be higher in seedlings growing below a conspecific versus heterospecific adult in two species (Table 3.5). Increased mortality of seedlings near adult trees has been recorded in dipterocarps by Liew & Wong (1973), and Chan (1980) found a correlation between mortality and distance in one of two trees each of *S. leprosula* and *S. macroptera*. Reviewing 24 studies of seedling mortality, Clark & Clark (1984) found

evidence of distance-dependent mortality in 15 studies. However, in the present study, the effect of proximity to a conspecific versus heterospecific large tree could often not be separated from other correlated factors. For example, differences existed between species in mean size of large trees. Between the two seedling groups (growing beneath conspecific versus heterospecific trees), differences existed in some species in frequency distributions of heights and distance to nearest large tree, and in density.

The picture is not clear, and many factors probably interact to produce differential mortality. There is also the problem that the current study offers only a brief 'snap-shot' of the processes involved in forest dynamics. Observed differences in mortality rates and in spatial distributions of seedlings in relation to large trees could be either the result of past differential mortality or the cause of the currently observed patterns of mortality (or both). The highest mortality rates are likely to occur just after germination, when differences in mortality will be largest. These effects will reduce over time following mass recruitment, and may have disappeared by the time of the present study.

CHAPTER 4

GROWTH OF SEEDLINGS

4.1 CALCULATION OF GROWTH RATES

Seedling growth rates were calculated from the differences in heights (cm) measured at successive enumerations. Estimates of growth are therefore based on net height difference rather than actual growth, but for convenience will be referred to as growth rates. A large proportion of seedlings had suffered stem breakage (Chapter 2.4). Many of these may have been growing actively before stem breakage, or have regrown subsequently and the calculated growth rates are the net result of these processes. This will have resulted in under-estimation of actual growth rates. Since stem breakage was largely caused by falling branches, it is likely to occur randomly in space and all species should be equally affected.

Growth rates were expressed in the following two ways. Relative Growth Rate (RGR, % yr^{-1}) estimates the change in height relative to initial height, and thus allows comparison of growth rates between individuals with different initial heights. It was calculated from:

$$RGR = (\ln H_2 - \ln H_1) / (t.100)$$

where H_1 is the original height, and H_2 the height after time t, the time elapsed in years between enumerations for each individual; t was found from:

$$t = (WK_2 - WK_1) / 52$$

where WK_1 and WK_2 are the corresponding dates of measurement, to the nearest week. A value of around 70 % yr^{-1} for RGR indicates a doubling of height over one year, and was around the maximum attained in the study (Chapter 4.5).

Absolute height increment may be a more relevant measure of seedling performance in terms of access to light and dominance over surrounding vegetation (Caldwell 1987). Annual absolute height increment, AHI, (cm yr^{-1}) was found from:

$$AHI = (H_2 - H_1) / t$$

Seedlings in Plot 2 were measured twice, giving growth estimates over a single interval (designated RGR and AHI). Plot 1 seedlings were measured three times, giving estimates of growth for two successive intervals, (first interval: RGR1 and AHI1; second interval: RGR2 and AHI2). A third estimate of overall growth in Plot 1 for both intervals combined (RGR3 and AHI3) was equivalent to the interval between Plot 2 measurements.

The individual growth rates were not normally distributed. In all species the distribution was leptokurtic with a long negative tail (Figure 4.1). Modal growth rate was zero in most species. The assumptions of parametric statistical procedures are not met, and therefore non-parametric statistics were used for all tests involving RGR and AHI.

4.2 INDIVIDUAL VARIATION

Frequency distribution curves of RGRs for different species in Plots 1 and 2, are shown in Figure 4.1, and illustrate the non-normal distribution of growth rates. The frequency distribution curves usually showed a strong peak at RGR values around zero, and rapidly decreased to a long and flat negative tail. At positive RGR values the curves fell off less steeply. Within this broad picture the shape of RGR frequency distribution curves differed between species and species groups.

Curves for slow growing species peaked at lower RGR values and were more leptokurtic than the curves for fast-growing species. In Plot 1, frequency distribution curves for *H. nervosa*, *V. sarawakensis* and the Dark Red Merantis, *S. fallax* and *S. pauciflora* peaked in the 0-2 % yr^{-1} RGR class and were strongly leptokurtic, with >20% of individuals in this class. The species with the lowest median growth rate, *V. sarawakensis*, had the highest percentage (41%) in the modal class. The curve for *P. malaanonan* also peaked in the 0-2 % yr^{-1} class, but was less leptokurtic than *V. sarawakensis*.

RGR frequency distribution curves for *S. johorensis* and the Light Red Merantis peaked in higher growth classes (2-4 % yr^{-1} in *S. johorensis* and *S. leprosula* and 4-6 %

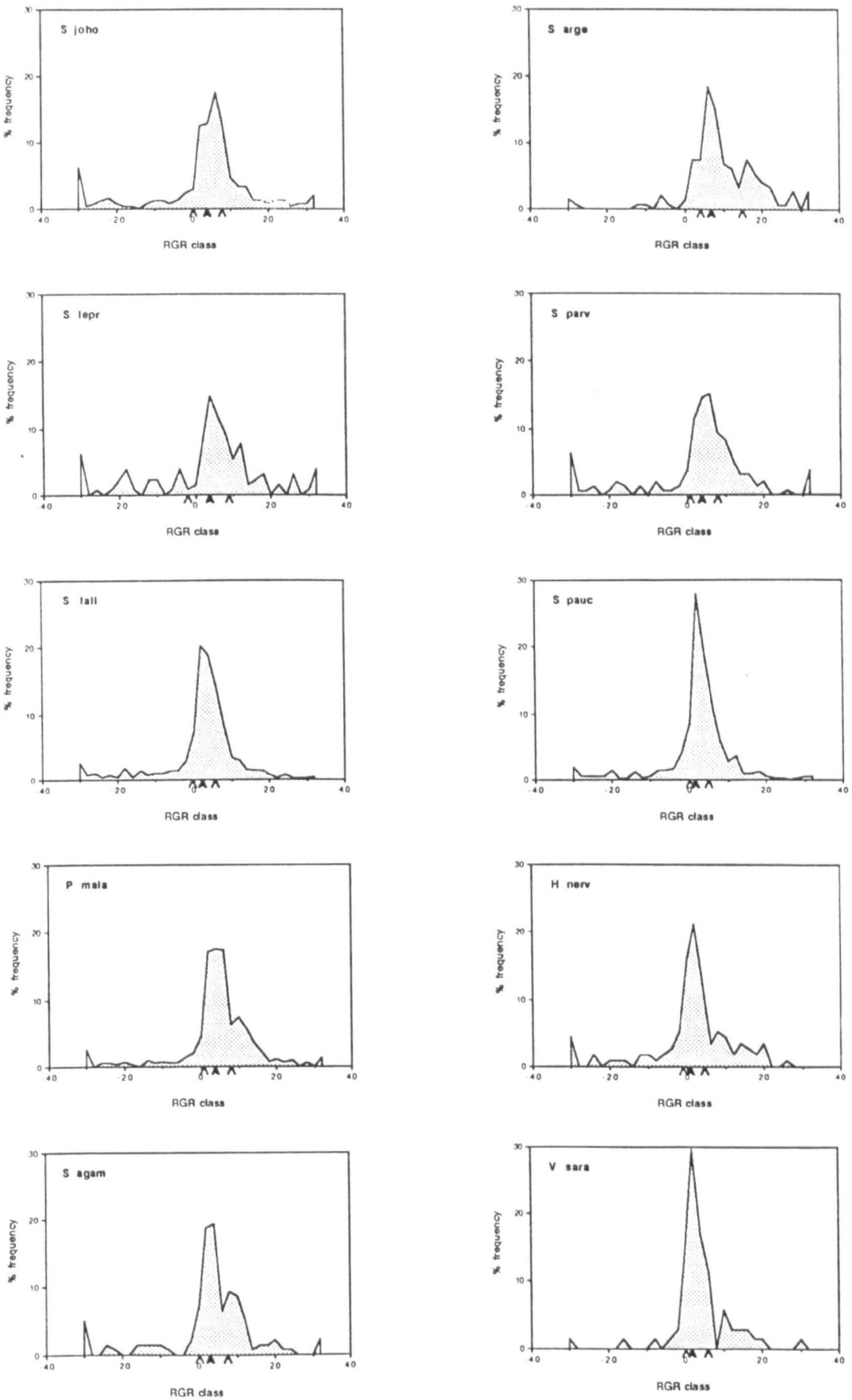


Figure 4.1 Frequency distributions of Relative Growth Rate (RGR, % yr^{-1},combined interval, Plot 1) in different species. Median RGR is marked by bold arrow, and smaller arrows mark upper and lower quartiles.

yr^{-1} in *S. argentifolia* and *S. parvifolia*), were less leptokurtic (all had 14-15% in the modal class), and had small secondary peaks in higher RGR classes. In these species, a larger proportion of individuals achieved high growth rates, whereas in slower growing species, most individuals grew slowly (as indicated by the larger percentage in the modal class) and very few had fast growth rates.

The shape of the frequency distribution curves guided the division of individuals into five growth categories for further analyses. The category with RGRs around zero, defined as dormant, ranged from >-4.0 % yr^{-1}, the point at which the curve in most species began to rise steeply, to +4.0 % yr^{-1}. The group with negative increments was further divided at -16.0 % yr^{-1} into 'heavily damaged' (≤-16.0 % yr^{-1}) and 'moderately damaged' (-16.0 to -4.0 % yr^{-1}) groups. The positive increments were divided into 'slow-growing' (>4.0 to 16.0 % yr^{-1}) and 'fast-growing' (>16.0 % yr^{-1}) seedlings.

4.3 MEAN GROWTH RATES

Variation in growth rates between individuals was great. The large changes in height, particularly the large negative increments, which occurred in all species, have considerable influence on the overall mean value. Therefore, median values were chosen as a more robust measure of central tendency. *S. johorensis* in Plot 1 illustrates this well: maximum and median growth rates were high relative to other species, but mean growth rate was low. The high number of large negative growth rates in this species (almost 9% of individuals had RGR <-30.0 % yr^{-1}) brought the mean RGR down to just above zero, compared to the median value of 3.6 % yr^{-1}. Mean growth rates for each species are reported (Table 4.1) to allow comparison with other studies.

Table 4.1 Mean (and standard deviation) of Relative Growth Rate (RGR, % yr^{-1}) and Annual Height Increment (AHI, cm yr^{-1}) for each interval in Plot 1, and in Plot 2. N1, N2, and N3 are the number of seedlings included in the calculation of RGR1, AHI1 (first interval), RGR2, AHI2 (second interval) and RGR3, AHI3 (total interval) in Plot 1.

	Plot 1			Plot 2	Plot 1						Plot 2		Plot 1						Plot 2	
	N1	N2	N3	N	RGR1		RGR2		RGR3		RGR		AHI1		AHI2		AHI3		AHI	
Species					mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
S joho	276	253	229	123	-0.2	39.29	-0.5	24.45	0.1	20.55	-0.1	15.22	-1.0	65.78	2.8	29.59	2.6	29.36	1.4	28.73
S arge	189	177	146	35	8.8	27.27	8.4	12.85	8.5	11.60	13.2	13.88	8.7	23.55	9.9	18.16	9.9	16.82	14.9	19.08
S lepr	145	134	128	15	-2.5	45.14	1.9	25.10	1.0	20.23	4.9	8.65	-4.3	78.20	6.9	41.18	3.8	33.27	5.0	6.54
S parv	172	171	158	87	-5.0	42.23	3.4	21.28	1.7	17.29	9.4	15.89	-4.9	51.06	5.3	29.71	3.8	24.13	9.0	24.03
S fall	522	572	502	92	-5.7	42.48	1.5	13.33	0.7	11.90	10.8	16.38	-9.1	62.98	1.1	25.03	0.4	19.82	12.1	32.20
S pauc	461	466	419	-	-1.5	51.58	0.9	11.67	1.0	9.68	-	-	-1.8	47.78	1.9	13.00	1.0	12.31	-	-
P mala	517	521	491	225	0.4	37.36	3.5	15.57	2.8	13.10	5.9	10.33	0.1	33.39	3.1	17.64	2.4	15.39	3.1	11.34
H nerv	113	130	113	261	-2.4	25.64	-0.9	20.97	-1.4	17.91	3.5	12.82	-4.2	39.59	2.6	21.67	-0.4	21.18	4.3	16.80
S agam	144	151	139	-	-2.8	22.93	0.1	20.55	0.6	16.90	-	-	1.3	34.95	1.4	18.41	1.2	17.74	-	-
V dul1‡	498	464	463	-	1.5	11.98	4.4	10.44	3.9	8.74	-	-	0.2	9.90	2.1	6.45	1.7	5.59	-	-
V dul2‡	*	*	129	-	*	*	*	*	2.6	11.94	-	-	*	*	*	*	0.4	1.27	-	-
V sara	71	76	71	64	-0.7	14.33	0.03	38.66	-0.4	30.72	2.0	11.0	-0.1	11.33	3.2	10.61	2.3	8.77	1.7	14.40
S pilo	-	-		22	-	-	-	-	-	-	7.2	10.13	-	-	-	-	-	-	7.9	13.21

‡ V dul1 - seedlings older than 1985 cohort
V dul2 - seedlings of 1985 cohort

* V dul2 height not measured at second enumeration

4.3.1 Mean Relative and Absolute Growth Rates

Mean RGR values for separate species are given in Table 4.1. The number of negative mean RGRs emphasises the impact of height loss on species populations. Over the first interval in Plot 1, (*ca.* five months), mean RGRs were negative in eight species, and over the second interval (14 months) similarly so in two species, *S. johorensis* and *H. nervosa*. Even over 22 months, overall mean RGR was negative in *H. nervosa* and *V. sarawakensis* in Plot 1 and *S. johorensis* in Plot 2.

Mean annual absolute height increments for different species are given in Table 4.1. Highest mean increment in Plot 1 (calculated over both intervals) was 9.9 cm yr^{-1} in *S. argentifolia*. *H. nervosa* had the only overall negative increment, -0.4 cm yr^{-1}. Over the first interval in Plot 1, mean increments were negative in seven species. Two Light Red Merantis had increments of less than -4.0 cm yr^{-1}. In contrast, the remaining LRM, *S. argentifolia*, averaged 8.8 cm yr^{-1} height gain. Largest negative mean increment was -9.9 cm yr^{-1} in *S. fallax*. Mean increments over the second interval were positive in all species. *S. argentifolia* seedlings gained on average almost 10 cm yr^{-1}, and the other two LRMs, over 5 cm yr^{-1}. Lowest mean increments were in *S. fallax* (1.1 cm yr^{-1}) and *S. agamii* (1.4 cm yr^{-1}). In Plot 2, highest mean increment was again in *S. argentifolia* (14.9 cm yr^{-1}). Second highest was *S. fallax*, averaging 12.5 cm yr^{-1}. No species had a negative mean increment. Lowest were *S. johorensis*, 1.4 cm yr^{-1} and *V. sarawakensis*, 1.7 cm yr^{-1}.

4.4 MEDIAN GROWTH RATES

4.4.1 Median Relative Growth Rates

Median RGRs for each species are given in Table 4.2. In both plots, *S. argentifolia* had the highest median RGR, and in Plot 1 was highest in both intervals. The other Light Red Merantis and *P. malaanonan* had moderately high RGRs. *S. leprosula* had the lowest growth rate of the three LRMs in both plots. Lowest growth rates overall in Plot 1 were in *H. nervosa*, *V. sarawakensis* and *S. pauciflora*. In Plot 2, lowest RGRs were in *V. sarawakensis* and *S. johorensis*. Growth of *S. fallax* in Plot 2

was higher than that of the Red and Light Red Merantis except *S. argentifolia*, while in Plot 1 it grew more slowly than the Red and Light Red Merantis.

4.4.2 Median Annual Height Increment

Median AHIs for different species are given in Table 4.2. In Plot 1 the highest increments overall were in the LRMs. All three species had median increments greater than 4 cm yr^{-1}. *S. fallax* had the highest median increment in Plot 2, 9.4 cm yr^{-1}. The LRMs again had annual increments greater than 4 cm. Of the LRMs, *S. argentifolia* had the highest median increment in Plot 2, 7.7 cm yr^{-1}, and *S. leprosula* the highest in Plot 1, 6.4 cm yr^{-1}. Lowest medians in Plot 1 were in *H. nervosa* and *V. dulitensis* (both 0.6 cm yr^{-1}), and in Plot 2, *V. sarawakensis* (0.6 cm yr^{-1}).

4.5 MAXIMUM GROWTH RATES

Large growth increments were recorded in seedlings exposed to some degree of canopy opening, usually small partial gaps produced by either falls of small canopy or understorey trees, or limbs falling from large trees. While these small openings increased the light available to seedlings, they were rarely complete gaps *sensu* Brokaw (1982). Since only a small proportion of individuals in a population achieve fast growth rates, the extreme values recorded are to a certain extent influenced by sample size: if few individuals of a species are present, the chance of an extreme value occurring is lower.

4.5.1 Fastest growing seedlings

Maximum relative and absolute height increments recorded in individuals of each species are given in Table 4.3. The largest net (non-annualised) increments recorded were 113 cm over 5 months for a seedling of *S. parvifolia*, 230 cm for a *S. johorensis* sapling over the second interval, and over the combined interval, 189 cm in

Table 4.2 Median Relative Growth Rate (RGR, % yr^{-1}) and Annual Height Increment (AHI, cm yr^{-1}) for first (RGR1, AHI1), second (RGR2, AHI2) and combined (RGR3, AHI3) intervals in Plot 1 and in Plot 2. Numbers of seedlings as in Table 4.1.

	Plot 1			Plot 2	Plot 1			Plot 2
Species	RGR1	RGR2	RGR3	RGR	AHI1	AHI2	AHI3	AHI
S joho	2.5	3.8	3.9	3.5	2.4	3.6	3.6	3.3
S arge	7.0	7.2	7.1	11.1	4.9	5.8	5.6	7.7
S lepr	4.2	4.7	4.1	5.3	4.7	7.2	6.4	5.6
S parv	1.5	5.3	4.2	7.2	1.9	5.8	4.7	4.0
S fall	0.9	2.5	2.4	8.9	2.0	2.9	2.8	9.4
S pauc	2.2	1.6	1.7	-	1.9	1.4	1.6	-
P mala	2.7	4.4	3.7	4.5	1.9	2.8	2.2	1.7
H nerv	0.0	1.2	0.2	4.0	0.0	1.1	0.6	2.8
S agam	3.4	2.1	2.6	-	3.7	2.2	3.1	-
V dul1↕	0.0	4.1	3.5	-	0.0	0.7	1.1	-
V dul2↕	*	*	3.3	-	*	*	0.6	-
V sara	0.0	1.8	1.3	1.1	0.0	1.8	1.6	0.6
S pilo	-	-	-	4.9	-	-	-	3.6

↕ V dul1 - Seedlings older than 1985 cohort
V dul2 - Seedlings of 1985 cohort

* V dul2 height not measured at second enumeration

Table 4.3 Maximum Relative Growth Rate (RGR, % yr^{-1}) and Annual Height Increment (AHI, cm yr^{-1}) achieved by individual seedlings in each species over the first (RGR1, AHI1), second (RGR2, AHI2) and combined (RGR3, AHI3) intervals in Plot 1, and in Plot 2.

	Plot 1			Plot 2	Plot 1			Plot 2
Species	**RGR1**	**RGR2**	**RGR3**	**RGR**	**AHI1**	**AHI2**	**AHI3**	**AHI**
S joho	69.7	73.0	55.7	30.7	165.9	166.1	152.6	74.7
S arge	68.7	49.9	41.6	43.9	80.4	96.1	88.9	70.8
S lepr	77.1	67.2	52.8	19.9	189.1	156.0	128.6	17.7
S parv	114.8	67.3	78.2	89.6	217.6	130.0	121.9	92.0
S fall	51.9	58.0	53.1	53.1	135.2	93.3	75.2	117.8
S pauc	86.3	50.7	38.2	-	123.3	117.0	88.9	-
P mala	75.9	62.5	53.4	66.6	115.8	136.5	101.9	122.3
H nerv	45.1	33.3	24.0	52.9	86.7	73.7	55.3	90.2
S agam	72.7	37.2	39.0	-	106.5	60.7	71.0	-
V duli	63.4	36.9	29.2	-	66.2	42.6	34.8	-
V sara	26.5	34.3	28.1	31.7	37.8	31.5	25.4	40.4
S pilo	-	-	-	35.2	-	-	-	58.1

S. parvifolia. The largest increment in Plot 2 was 157 cm in a sapling of *P. malaanonan*. Seven species in Plot 1, and two in Plot 2 had individuals which exceeded 1 m yr^{-1}. Maximum annualised increment recorded was 218 cm yr^{-1}, in *S. parvifolia* over the first interval in Plot 1.

The species composition of the fastest growing individuals in Plot 1 was examined. AHI was used, since individuals with large height increments are increasing their exposure to light and are likely to be competing well with neighbouring plants. Individuals with large increments were usually tall saplings growing in a canopy opening, and could be described as 'most likely to succeed', whereas large values of RGR could be attained by small seedlings growing only a few centimetres.

The 200 fastest growing individuals in Plot 1 were listed, representing approximately 5% of the total seedling population in each plot. Species compositions are given in Table 4.4. The observed number of individuals of each species in the fastest growing group was compared with an expected number found from the proportional abundance of each species (including only individuals with increments measured over the interval), using a χ^2 goodness-of-fit test. A second group of 'fastest-growing seedlings' was selected in Plot 1, this time in a stratified manner, choosing the fastest-growing seedling from each 10 x 10 m quadrat, and species composition was again compared with the expected species composition.

Results

There were significantly more seedlings of the three LRMs and *S. johorensis* in the fastest-growing group than would be expected from the overall species proportions (Table 4.4). Two species had significantly fewer seedlings than expected in the fastest-growing group: *S. pauciflora* and *V. dulitensis*. In the stratified fastest-growing group, only one species differed from the expected proportions: *V. dulitensis* again had fewer seedlings than expected. In all other species, the proportions of species in the fastest-growing group were not different from the overall plot proportions.

Table 4.4 Species composition of the fastest growing seedlings in Plot 1. The 200 individuals with the highest Annual Height Increments (second interval) are included. The stratified group includes the fastest-growing seedling in each 10x10 m subplot. The expected number was calculated from the proportion of each species in the plot and compared with the observed number with a χ^2 test.

Species	N	Expected	Fastest-growing seedlings			Stratified fastest-growing seedlings		
			Obs	χ^2	P	Obs	χ^2	P
S joho	253	16	25	4.86	*	21	1.46	N.S.
S arge	177	11	25	16.33	***	13	0.26	N.S.
S lepr	134	9	22	21.15	***	12	1.39	N.S.
S parv	171	11	21	9.32	**	17	3.40	N.S.
S fall	572	35	41	0.60	N.S.	35	0.07	N.S.
S pauc	466	30	11	11.81	***	29	0.02	N.S.
P mala	521	33	23	3.16	N.S.	35	0.09	N.S.
H nerv	130	8	9	0.06	N.S.	10	0.34	N.S.
S agam	151	10	10	0.01	N.S.	14	1.98	N.S.
V duli (>20cm)	464	30	10	12.99	***	6	18.82	***
V sara	76	5	2	1.67	N.S.	5	0.27	N.S.
Others	35	2	1	0.67	N.S.	3	1.42	N.S.
Total	3150	200	200	-		200	-	

4.5.2 Comparison of maximum and median growth rates

Maximum rates were between 16 and 100 times higher than median rates in Plot 1, and 3-72 times higher in Plot 2. The low maximum rates recorded in *S. argentifolia* and *S. leprosula* in Plot 2 compared to the values in Plot 1 are probably a function of the low numbers present in Plot 2.

In Plot 1, each species' rank order of maximum growth rates was similar to its rank order by median growth rates (Spearman r_s=0.627, n=11, P<0.05). Species with high median growth rates had high maximum growth rates. An exception to this was *S. argentifolia*, which had the highest median growth rate but was ranked seventh for maximum growth rate. The two DRMs were ranked more highly for maximum rate than median rate.

In Plot 2, rankings for median and maximum rate were not correlated (Spearman r_s=0.358, n=9, p>0.05). Interestingly, *S. argentifolia* again had the highest median growth and was ranked lower (fifth) in maximum growth. One other LRM, *S. leprosula*, was ranked higher for median than maximum growth, and had the lowest maximum growth rate of all species (but only 15 seedlings were recorded in this species). Both *P. malaanonan* and *H. nervosa* were more highly ranked for maximum than median RGR.

4.6 HEIGHT LOSS AND ZERO GROWTH

Over each enumeration period a proportion of seedlings lost height, and others had measured increments of around zero. Dipterocarp seedlings are known to remain dormant under certain conditions for long periods (Baur 1964). Height loss (defined as RGR less than -4.0 % yr^{-1}) appeared to be caused mostly by falling trees and branches. Other possible reasons included die-back due to pathogen infection, stem-boring herbivores, or water stress.

Increments of ±1 cm may have been recorded due to measurement error for seedlings that were actually dormant, and similarly, real height changes of ±1 cm may have been recorded as zero. The zero growth category will also include seedlings

which were not truly dormant, but in which growth equalled height loss between enumerations, resulting in a net height difference of zero. For these reasons, (and those stated in Section 4.2) the zero growth category was expanded to include the band from -4.0 to +4.0 % yr^{-1}.

Figure 4.2 shows the percentage of seedlings in each species in Plot 1 in the five growth categories (heavy and moderate damage, dormant, and slow and fast growth as defined in Section 4.2 above) over the total enumeration interval.

4.6.1 Height loss

The greatest absolute height losses recorded between enumerations were 407 cm and 365 cm (both *S. pauciflora*) in Plot 1 and 205 cm (*P. malaanonan*) in Plot 2. Overall 88 out of 932 individuals (9.5%) lost height in Plot 2, significantly fewer than in Plot 1, where 331/2429 (13.6%) lost height over the equivalent interval (χ^2=10.38, df=1, P<0.01 for the 2x2 contingency table). Over the combined interval in Plot 1, the proportion of seedlings with negative increments reached almost 25% in *S. leprosula*. Lowest proportions were in *V. sarawakensis* (5.6%), *S. argentifolia* (6.2%) and *V. dulitensis* (9.3%). In contrast, *V. sarawakensis* had one of the highest proportions of height loss in Plot 2 (21%), second to *H. nervosa* (22%). In the remaining species in Plot 1, 10-18% of individuals lost height. In Plot 2, less than 10% lost height in most species, and lowest proportion was in *S. argentifolia* (3%).

4.6.2 Zero growth

In Plot 1, 1123 out of 2675 seedlings (42.9%) were in the zero growth, or dormant, category over the first interval (5-6 months) and 1181/2675 (44.9%) over the second interval (18 months). Over the combined interval, 1061/2419 (43.9%) seedlings had zero growth, significantly more than in Plot 2, 330/932 (35.4%) (χ^2=19.8, df=1, P<0.001).

In both plots, frequencies of zero growth were highest in slow-growing species, and lowest in faster-growing species. *V. sarawakensis* had the highest proportion of dormant seedlings in both plots: 65% in Plot 1 and 55% in Plot 2. *S.*

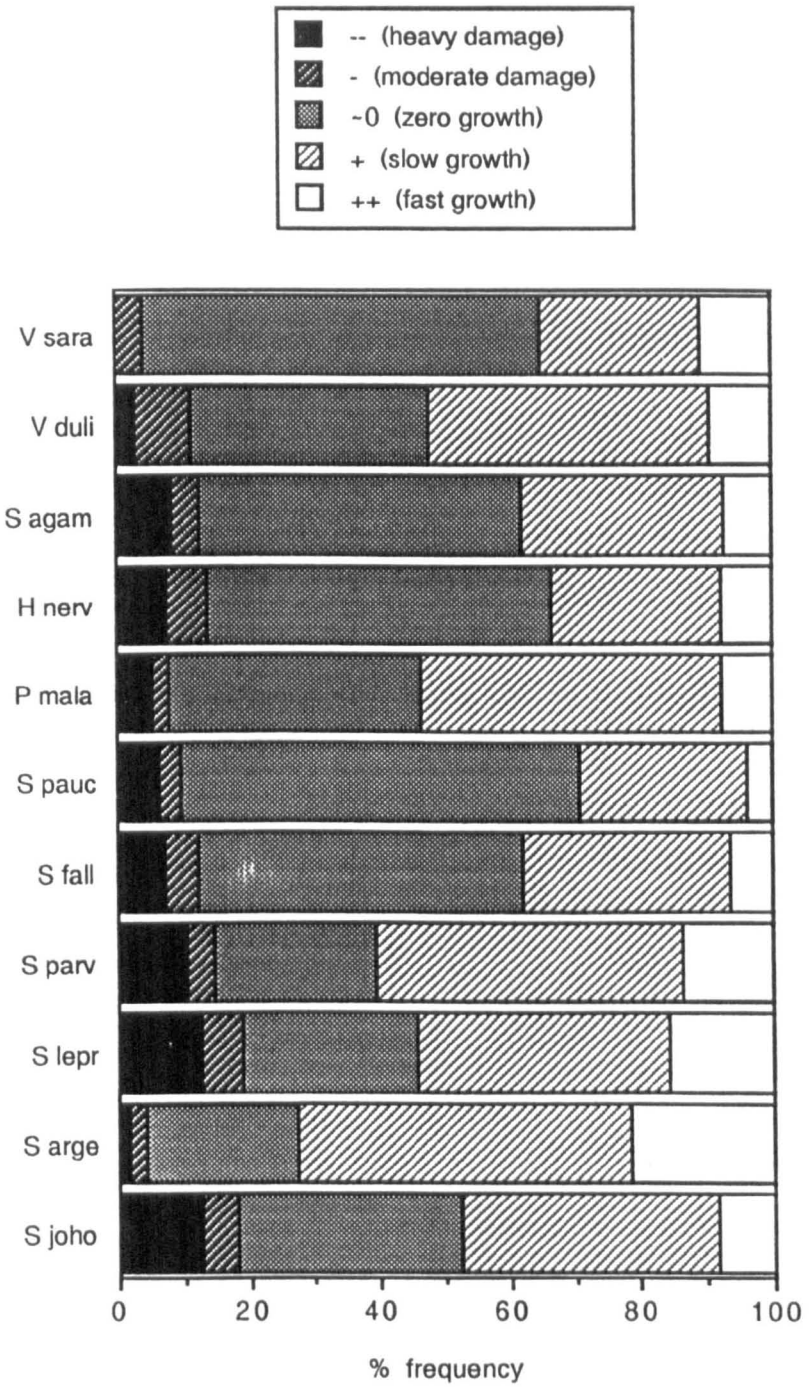


Figure 4.2 Percentage of seedlings of different species in each growth category (defined in Section 4.2) in Plot 1.

argentifolia had the lowest proportion of dormant seedlings in both plots (16% and 17%, Plots 1 and 2 respectively). The LRMs had below average numbers of dormant seedlings in both plots (χ^2 goodness-of-fit tests, $P<0.05$).

4.6.3 Growth category and size

The percentage of seedlings in the five growth categories in six height classes in Plots 1 (combined interval) and 2 are illustrated in Figure 4.3. Frequency of height loss increased with height in both plots (Figure 4.3). Of the smallest seedlings (≤50 cm tall), 6% lost height in both plots, rising to 24% (Plot 2) and 23% (Plot 1) in the largest size class (>400 cm). Frequency of zero growth peaked in seedlings of intermediate size in both plots (151-200 cm in Plot 1, and 101-151 cm in Plot 2). Around 30% of the smallest seedlings (≤50 cm tall) in both plots had zero growth.

In both plots, the frequency of fast-growing seedlings was highest in the smallest seedlings (13.3% and 15.3%, Plots 1 and 2), and lowest in the largest size class (3.6% and 4.8%, Plots 1 and 2). In intermediate size classes there were differences between plots. In Plot 1 the proportion of seedlings with positive growth dropped to between 4 and 7% in these classes, whereas in Plot 2, the proportion remained between 11 and 15%.

4.6.4. Comparison of Meranti groups

Percentage of Light and Dark Red Meranti seedlings in the five growth categories in six height classes are shown in Figure 4.4. In both groups, frequency of positive growth rates was highest in seedlings ≤50 cm tall, and dropped markedly to lower levels in larger size classes. Negative increments became more frequent with increasing size class, and in both groups were most frequent in the 151-200 cm height class. Zero increments were most frequent in small seedlings (≤50 cm tall) in both groups, but the rate in DRMs (43%) was more than double that in LRMs (20%). Between 53% and 39% of larger DRMs (>200 cm tall) had zero increments, compared to around 30% of LRMs. Overall, the frequency of positive increments was lower, and that of zero increments higher in the DRMs.

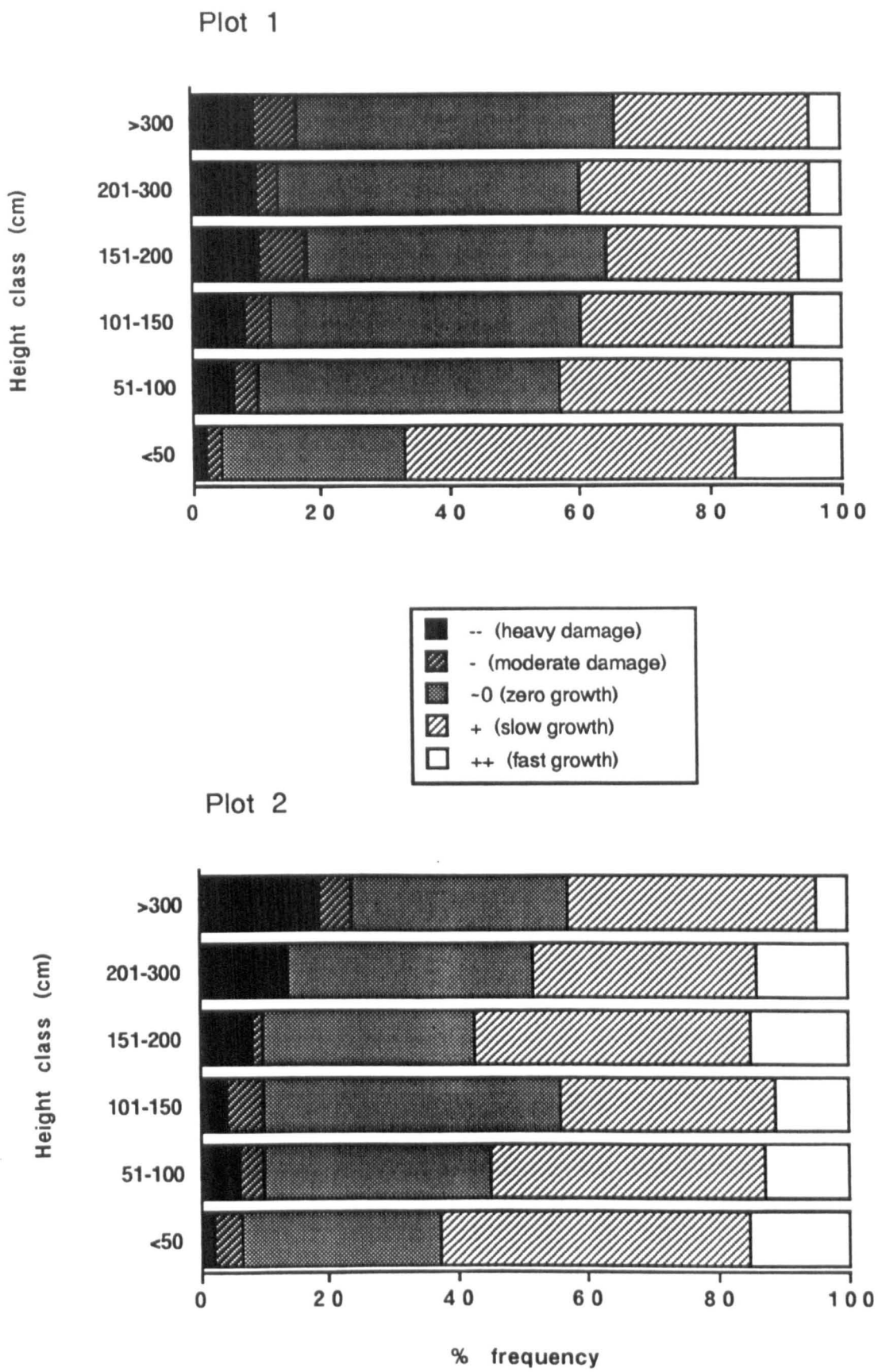


Figure 4.3 Percentage of seedlings of all species pooled (excluding *Vatica dulitensis* in Plot 1) in each growth category for six height classes in Plots 1 and 2. Growth categories are defined in Section 4.2.

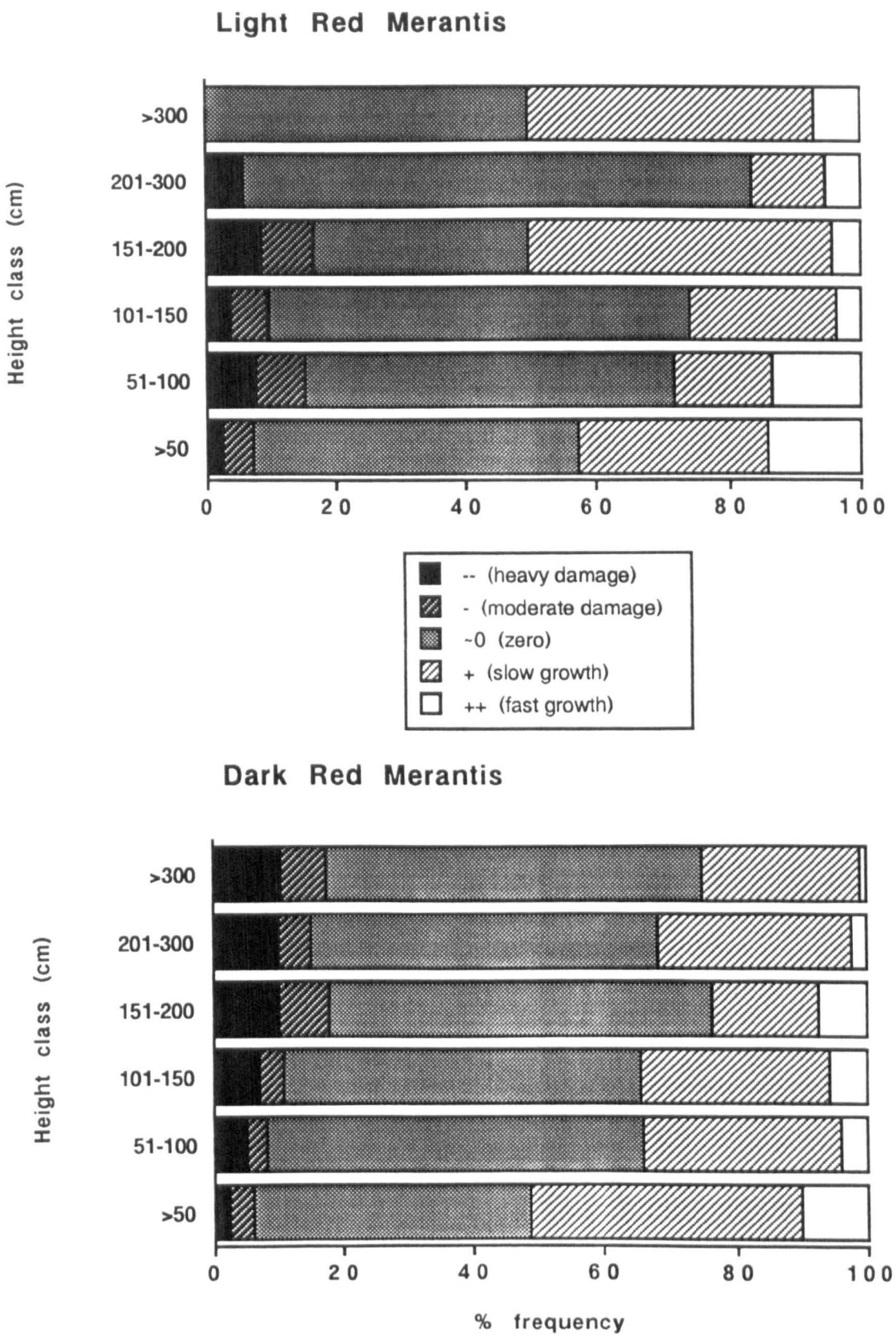


Figure 4.4 Percentage of seedlings in each growth category in Light and Dark Red Merantis for six height classes in Plot 1. Growth categories are defined in Section 4.2.

4.7 VARIATION IN GROWTH WITH SIZE

4.7.1 Variation in relative growth between species

Median RGRs for six height classes in different species are shown in Figure 4.5. Median RGR generally decreased with increasing initial height class. In almost all species median RGR was highest in the smallest height class (≤50 cm), the only exception being *H. nervosa* which had highest RGR in 151-200 cm saplings. The pattern of changing RGR with height class varied between species.

In several species (*S. leprosula*, *S. fallax*, *S. pauciflora*, *P. malaanonan* and *S. agamii*) median growth rate decreased rapidly with increasing height, growth rate being similar in the four largest height classes. In *S. parvifolia* growth decreased rapidly in the larger height classes and median growth rate was zero in the largest saplings (>300 cm). In contrast, growth in the largest height classes in *H. nervosa* and *V. sarawakensis* was higher than in the preceding height class. In both *S. johorensis* and *S. argentifolia* there was a secondary peak in median growth in saplings 201-300 cm. Median growth rates of small seedlings were highest, at about 10 % yr^{-1}, in the three LRMs, *S. agamii* and *S. fallax*. The lowest rate, 0.0 % yr^{-1}, was in *V. sarawakensis*. In other species, the rate was 3-6 % yr^{-1}.

4.7.2. Height increment and initial height

Variation in median AHI in six height classes is shown in Figure 4.5 for different species in Plot 1. Changes in median AHI with increasing height class were very varied between species. *S. argentifolia* and *S. johorensis* were similar, median AHI increasing to highest values in seedlings 2-3 m tall, and decreasing in seedlings over 3 m tall. In *S. leprosula* and *P. malaanonan*, median AHI increased steadily with increasing height and was highest in seedlings over 3 m tall. *S. parvifolia* showed a very different pattern: median AHI was highest in seedlings 1.5 to 2 m tall, and

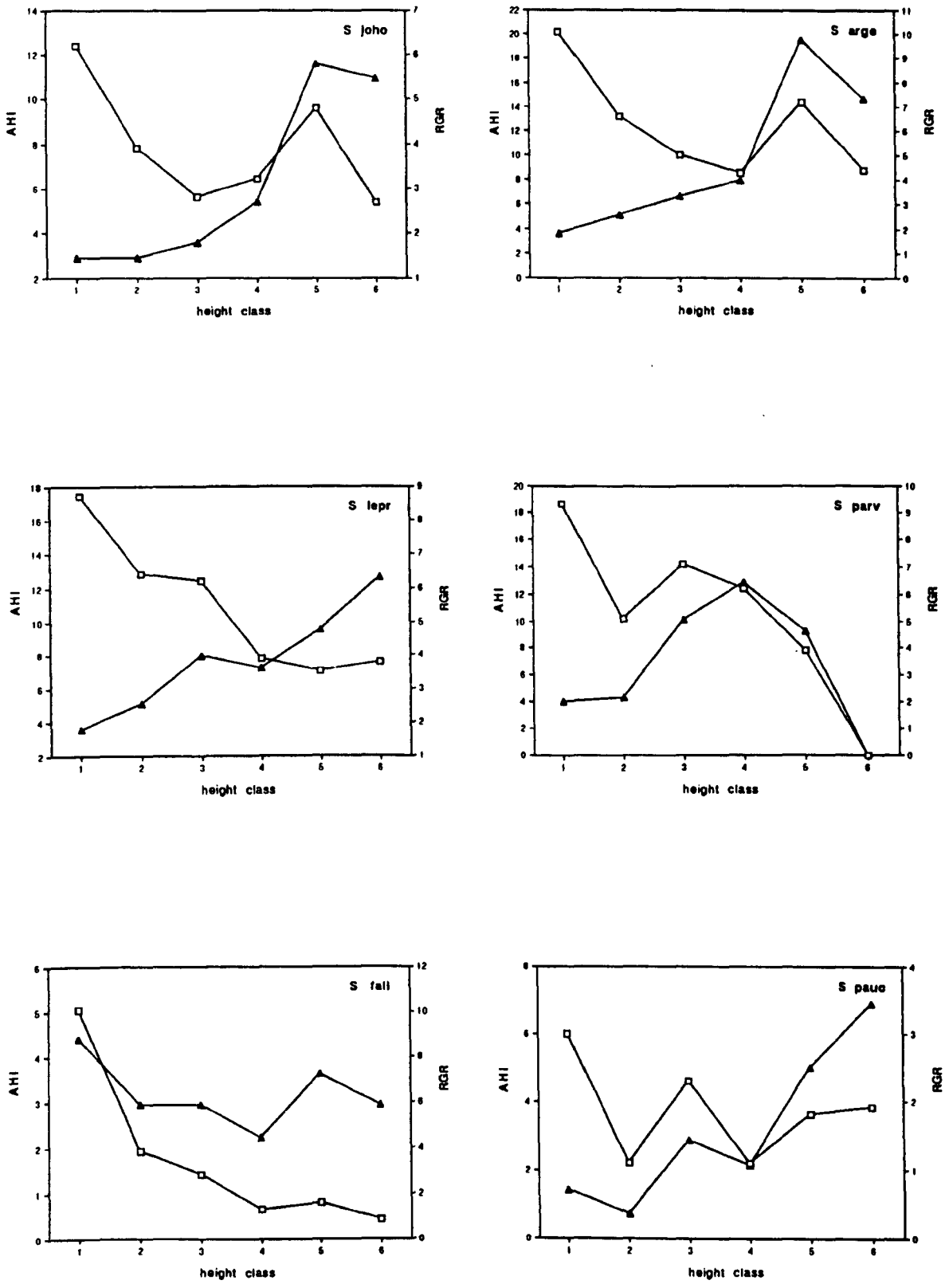
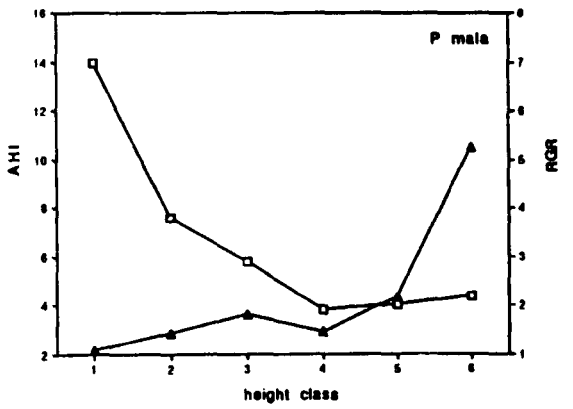
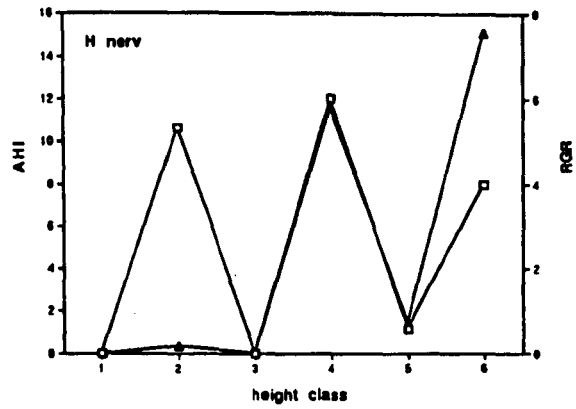
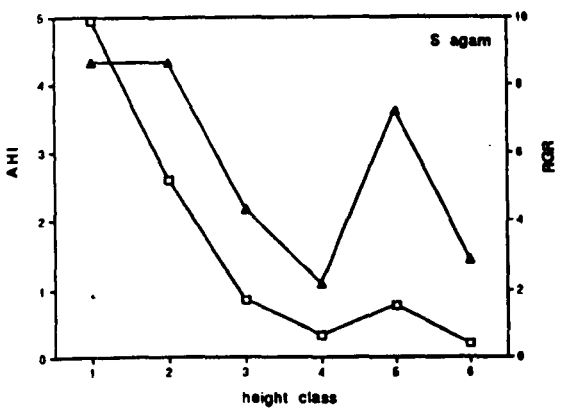
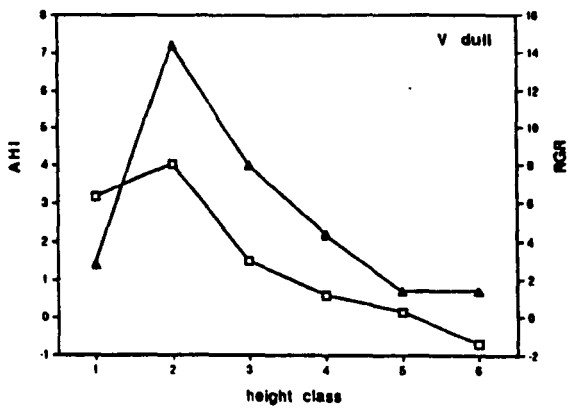


Figure 4.5 Median Relative Growth Rate (RGR, % yr^{-1}, □) and median Annual Height Increment (AHI, cm yr^{-1}, ▲) in six height classes in different species. Height classes 1 to 4 are in 50 cm intervals; class 5, 201-300 cm; class 6, >300 cm.
(a) Plot 1, second interval.









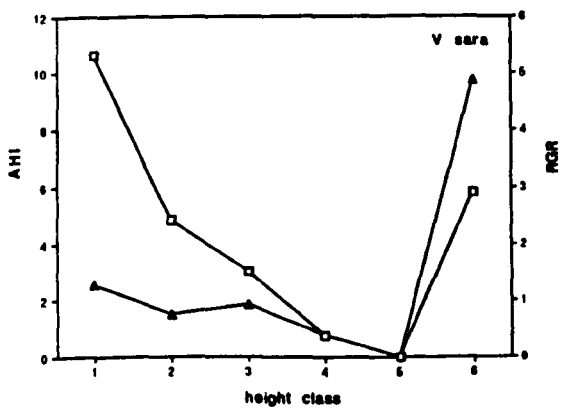


Figure 4.5 (continued) Median Relative Growth Rate (RGR, % yr^{-1}, □) and median Annual Height Increment (AHI, cm yr^{-1}, ▲) in six height classes in different species. Height classes 1 to 4 are in 50 cm intervals; class 5, 201-300 cm; class 6, >300 cm.
(a) Plot 1, second interval.

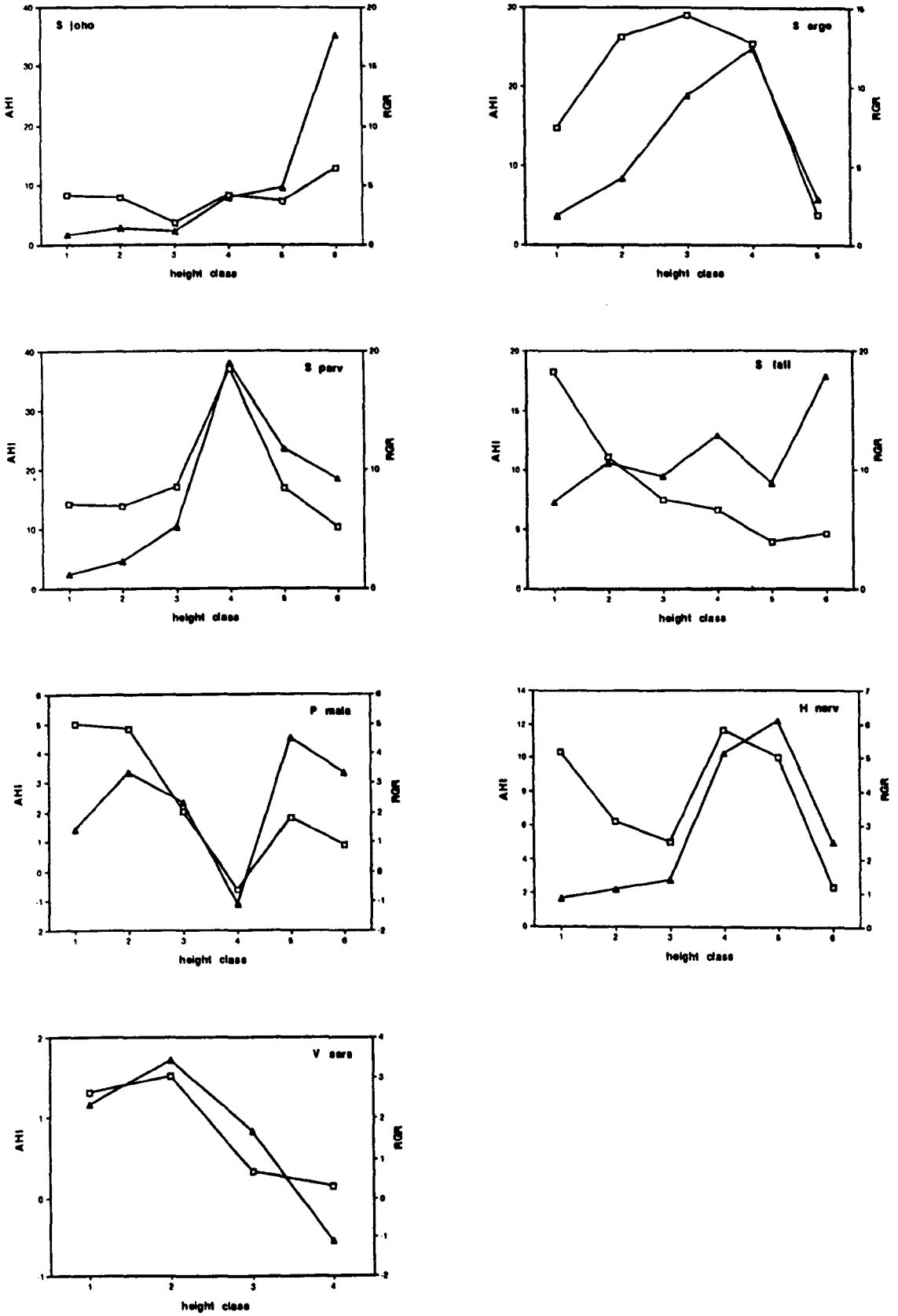


Figure 4.5 (continued) Median Relative Growth Rate (RGR, % yr^{-1}, □) and median Annual Height Increment (AHI, cm yr^{-1}, ▲) in six height classes in different species. Height classes 1 to 4 are in 50 cm intervals; class 5, 201-300 cm; class 6, >300 cm.

(b) Plot 2

decreased sharply in seedlings over 2 m. In contrast, median AHI was lowest in seedlings 1.5-2 m tall in *S. pauciflora*. In *P. malaanonan*, *H. nervosa* and *V. sarawakensis*, there was a rapid rise in median AHI between seedlings less than 3 m and greater than 3 m tall. In the smallest seedlings (<50 cm), median AHI was highest (3-4 cm yr^{-1}) in the three LRMs, *S. fallax* and *S. agamii*. In the largest seedlings (>3 m), median AHI exceeded 10 cm yr^{-1} in *S. johorensis*, *S. argentifolia*, *S. leprosula*, *H. nervosa* and *P. malaanonan*. Highest median AHI of any size class / species combination in Plot 1 was 19.5 cm yr^{-1}, attained by *S. argentifolia* saplings 2-3 m tall.

4.8 VARIATION BETWEEN PLOTS

Differences in species growth rates, both RGR and AHI, between Plot 1 and Plot 2 were tested with the Mann-Whitney U-test (using growth rates in Plot 1 calculated over both time intervals combined).

Four species, *S. parvifolia*, *S. fallax*, *P. malaanonan* and *H. nervosa* had significantly higher RGRs in Plot 2 than in Plot 1 ($P<0.05$). AHI was significantly higher in *S. fallax* and *H. nervosa*, in Plot 2 ($P<0.05$). No species grew faster in Plot 1. Neither RGR nor AHI of the remaining species differed significantly between the plots ($P>0.05$).

Neither median species RGR nor AHI were rank correlated between Plots 1 and 2 (RGR: Spearman $r_s=0.633$, $0.05<P<0.10$; AHI: $r_s=0.557$, $p>0.1$; $n=8$). The main differences in rank were in *S. fallax*, second highest RGR in Plot 2 but sixth ranked in Plot 1, and in *S. johorensis* and *H. nervosa*. *P. malaanonan* was ranked fifth in both plots, but had significantly higher RGR in Plot 2. *S. johorensis* was ranked fourth for RGR in Plot 1, but seventh in Plot 2, though RGR did not differ significantly between plots.

Comparison of growth rates between plots is complicated by differences in height distributions between plots (Chapter 2.3), since growth rates varied with size. The between-plot comparisons of growth rate were repeated for five height classes within each species, using Mann-Whitney U-test.

Growth rates did not differ between plots in any height class in three species:

S. johorensis, *S. leprosula* and *V. sarawakensis*. Significant differences were largely confined to seedlings below 150 cm tall, with one exception: 150-200 cm *S. argentifolia* seedlings grew faster in Plot 2. *P. malaanonan* grew faster in Plot 1 in the two smallest height classes. *S. fallax* seedlings 50-150 cm tall grew very much faster in Plot 2. In the remaining species/height classes with significant differences, growth rates were faster in Plot 2.

4.9 TEMPORAL VARIATION IN GROWTH RATES (Plot 1)

4.9.1 Variation in growth rates over time

Differences in RGRs between the first and second intervals within each species in Plot 1 were tested with Wilcoxon's matched-pair sign test (using the large sample approximation of SPSS^X [SPSS^X Inc. 1983]).

One species, *S. pauciflora*, grew significantly faster over the first interval ($Z=-2.241$, $P<0.05$), while two species grew significantly faster during the second interval: *S. parvifolia* and *V. sarawakensis* ($Z=-2.939$ and $Z=-2.106$ respectively, $P<0.05$ in both cases). Growth rates in the remaining species did not differ between the two intervals.

Median species growth rates in the two intervals were significantly rank correlated across species (Spearman $r=0.750$, $n=11$, $P<0.01$): the fastest growing species continued to grow fastest and the slowest remained slow-growing.

4.9.2 Correlation of successive growth rates

Scatter plots of RGR2 versus RGR1, and correlation coefficients, for different species are shown in Figure 4.6. Few individuals in any species sustained a high growth rate over both intervals. Both RGR and AHI were significantly rank correlated over the successive intervals in five species. In addition, in *S. parvifolia*, AHIs were correlated, but RGRs were not, and in *S. fallax*, RGRs were correlated

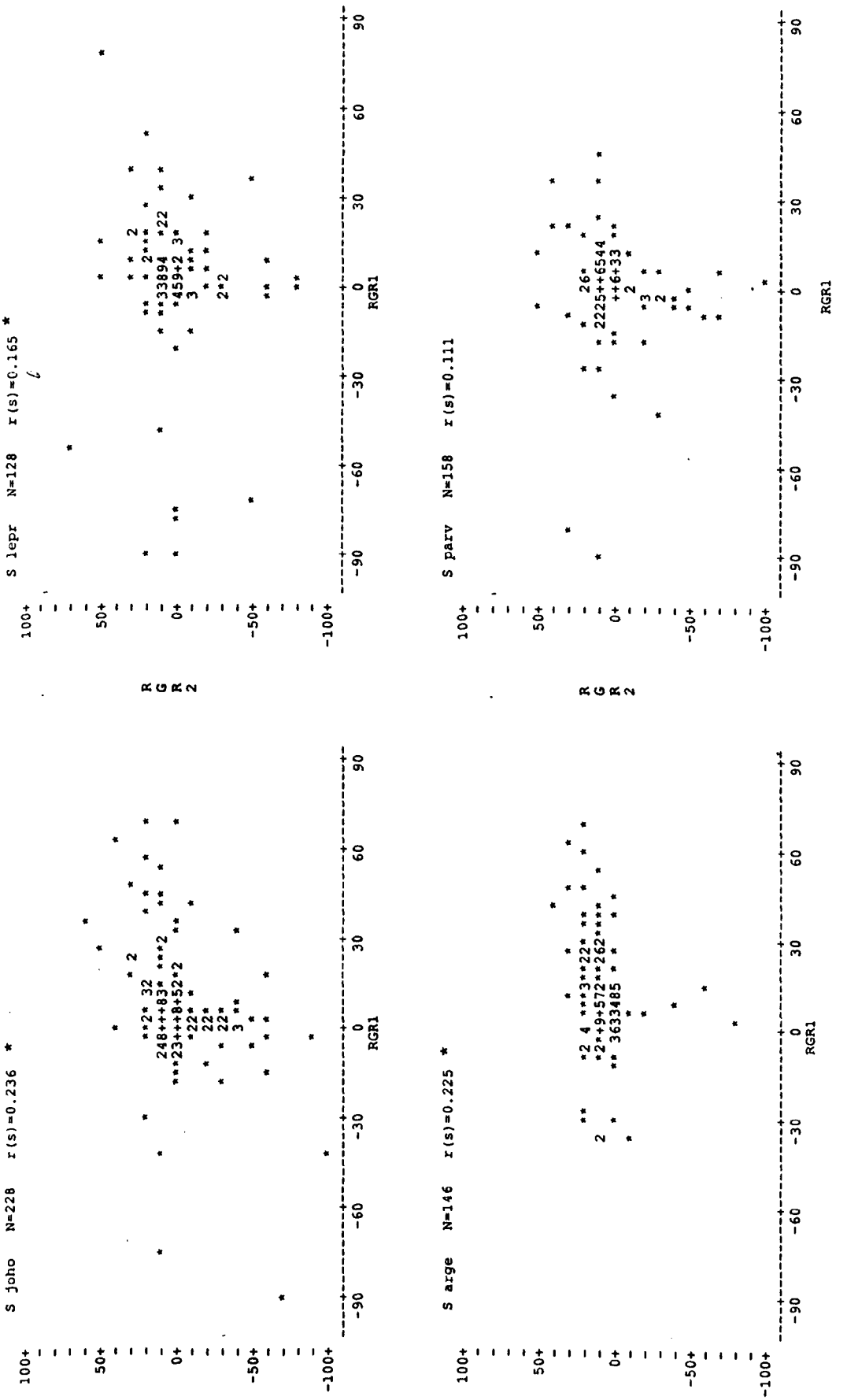


Figure 4.6 Relationship between Relative Growth Rates (% yr^{-1}) in the first (RGR1) and second (RGR2) intervals in Plot 1, and values of the Spearman rank correlation coefficient, r_s. * indicates significant correlation ($P<0.05$). numbers in the graphs give the number of seedlings sharing the same rates.

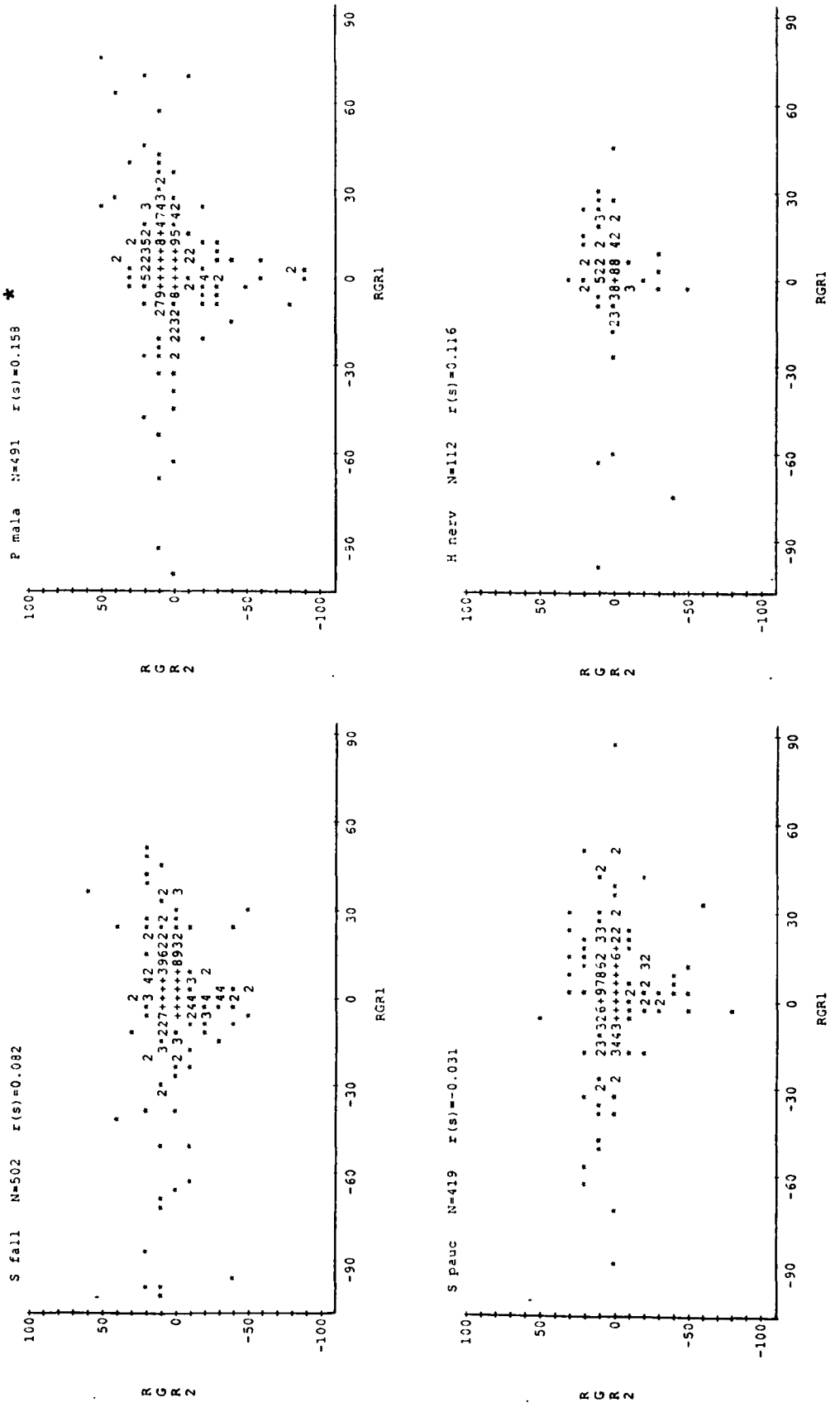


Figure 4.6 (continued) Relationship between Relative Growth Rates (% yr^{-1}) in the first (RGR1) and second (RGR2) intervals in Plot 1, and values of the Spearman rank correlation coefficient, r_s. * indicates significant correlation ($P<0.05$). numbers in the graphs give the number of seedlings sharing the same rates.

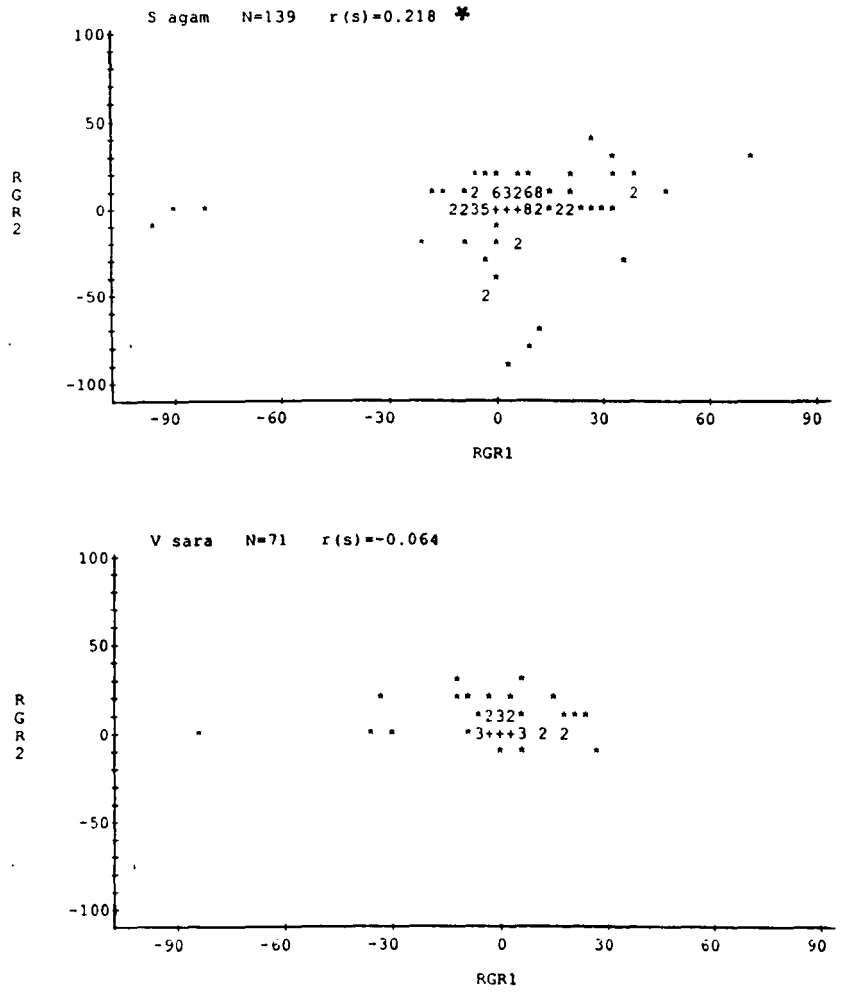


Figure 4.6 (continued) Relationship between Relative Growth Rates (% yr^{-1}) in the first (RGR1) and second (RGR2) intervals in Plot 1, and values of the Spearman rank correlation coefficient, r_s. * indicates significant correlation ($P<0.05$), numbers in the graphs give the number of seedlings sharing the same rates.

while AHIs were not. The species in which neither measure of growth rates were correlated were the slowest-growing species: *V. sarawakensis*, *H. nervosa* and *S. pauciflora*.

To establish whether growth rates were more consistent in any particular size class of seedling, correlations between first and second interval growth rates (RGRs and AHIs) were calculated for six height classes in each species. Significant correlations ($P<0.01$) between RGRs occurred in at least one height class in each species except *V. sarawakensis*. Correlations between AHIs were fewer, and in four species, (*V. sarawakensis*, *H. nervosa*, *S. pauciflora* and *S. fallax*) were not significant in any height class. There were more weakly negative correlations in the slowest-growing species.

4.10 GROWTH RATE IN RELATION TO PROXIMITY TO ADULT TREES.

Under the 'compensatory mechanisms' hypothesis of Connell *et al.* (1984), rarer species are favoured over commoner species at a site through increased rates of reproduction, survival or growth. The hypothesis predicts that commoner species have lower rates of survival and / or growth. Evidence was sought by comparing growth rates (using Mann-Whitney U-test) in seedlings growing within 10 m of ('near') a conspecific versus heterospecific adult tree, and with those growing more than 10 m from any large dipterocarp tree.

Results

There was very strong depression of growth rate in *S. pauciflora* in seedlings growing within 10 m of a conspecific adult compared to those growing within 10 m of another species or more than 10 m from any large dipterocarp (Table 4.5). There was no difference between the latter two groups. Median RGR was 58% lower and AHI 72% lower near a conspecific adult. In contrast, in both *S. leprosula* and *S. parvifolia*, growth rates were significantly higher in the few seedlings that grew near a conspecific tree. In *S. leprosula*, growth rate was also higher in seedlings growing more than 10 m from any large dipterocarp.

Table 4.5 Comparison of Relative Growth Rate (RGR, % yr^{-1}) and Annual Height Increment (AHI, cm yr^{-1}) between seedlings growing beneath (≤10 m from) conspecific versus heterospecific large (≥100 cm gbh) dipterocarp trees and seedlings growing > 10 m from any large dipterocarp. Pair-wise comparisons of growth rates were done with Mann-Whitney U-test. P^1 is significance value from comparison between seedlings beneath conspecific versus heterospecific trees; P^2, beneath conspecific versus > 10 m from any dipterocarp tree; P^3, beneath heterospecific versus >10 m from any dipterocarp tree.

	beneath conspecific			beneath heterospecific			> 10m from any dipterocarp			P^1		P^2		P^3	
Species	n	RGR	AHI	n	RGR	AHI	n	RGR	AHI	RGR	AHI	RGR	AHI	RGR	AHI
S joho	86	3.7	3.6	63	4.0	4.3	104	3.3	3.6	NS	NS	NS	NS	NS	NS
S arge	3	22.2	7.8	105	6.9	5.1	69	7.2	5.8	*	NS	*	NS	NS	NS
S lepr	2	6.3	7.2	91	3.9	6.5	41	6.7	10.1	NS	NS	NS	NS	*	*
S parv	8	14.9	13.0	98	5.3	5.0	65	4.8	7.1	*	NS	*	NS	NS	NS
S fall	88	2.7	2.9	313	2.5	3.0	171	2.5	2.9	NS	NS	NS	NS	NS	NS
S pauc	116	1.1	0.7	132	2.6	2.5	218	1.5	1.4	**	***	NS	NS	*	**
P mala	1	-	-	282	4.4	2.8	238	4.4	2.8	-	-	-	-	NS	NS
H nerv	24	0.0	0.0	26	0.0	0.0	80	2.5	2.2	NS	NS	*	*	**	**
S agam	0	-	-	83	1.1	1.4	68	4.1	4.3	-	-	-	-	**	***

The growth patterns of *S. agamii* and *H. nervosa* seedlings support the idea that growing near any large tree is deleterious: in both species, growth was highest in seedlings growing more than 10 m from any large dipterocarp (in *S. agamii* none grew within 10 m of a conspecific tree).

4.11 GROWTH SIMULATION

Growth simulation (Lieberman & Lieberman 1985) was used to construct growth curves for different species. The method is a stochastic bootstrapping technique which 'grows' model seedlings by repeatedly sampling size-specific height increments from the data set. The method is described in detail in Lieberman & Lieberman (1985).

Growth simulation produces similar results to periodic annual increment, PAI (Lieberman & Lieberman 1985, M. Johnston, *pers. comm.*). PAI uses mean growth rates (usually annualised increments) within size classes, and depends on the distribution of growth rates within size classes (which are often skewed) and on choice of class size. One approach is to use the n best increments, where n is the number of trees in the next larger size class (Nicholson 1965a). Growth simulation provides estimates of median growth rates, as well as ranges, and maximum and minimum values which reflect the variation in the observed growth increments. Because the method samples the observed increments stratified by seedling height, the simulated curves show the variation in growth rates with size.

4.11.1 Method

The seedling data, in the form of height at two enumerations are ordered by initial height. Data from the second enumeration in Plot 1 were used. The starting size of the model seedling is chosen at random from the first group of seedlings. Its size after the first growth period is the height reached by the chosen seedling at the

second enumeration. The next increment is chosen at random from a window centred on the seedling which matches most closely the new height of the model seedling. The increment of this seedling is added to the model seedling. This is repeated, adding 18 months of age at each iteration, until the model seedling reaches the maximum height observed, creating a single growth trajectory. This was repeated 2000, 4000 or 16000 times, depending on the size of the data set. From the growth trajectories, maximum, minimum and median growth rates were estimated, together with the minimum time taken to reach 5 m height. Maximum and median rates were compared with the rates calculated from the data (Table 4.2).

One problem with the seedling data was the large number of negative increments. Before running the simulations, negative increments were set to zero. This would not affect estimates of maximum growth rates, but would result in estimated median growth being higher than observed figure.

4.11.2 Results

The simulated growth curves are illustrated in Figure 4.7. Estimates derived from the simulated curves of median, maximum and minimum growth rates, and time taken to reach 5 m height are given in Table 4.6.

A measure of variability in growth rates is the vertical distance between the maximum and minimum trajectories. The distance tended to be less in slow- growing species than in fast-growing species, and the 90% limits correspondingly broader. In fast-growing species, the minimum trajectory showed an increase in growth rate with increasing height. In slow-growing species, the minimum rate was more constant over the range of height.

Median growth rates varied more with height in the LRMs, *S. johorensis* and *P. malaanonan* than in the slower-growing species. Estimates of median growth rates (Table 4.6) are in the range 8.7 cm yr^{-1} (*V. sarawakensis*) to 53.5 cm yr^{-1} (*S. agamii*) and 52.5 cm yr^{-1} (*S. johorensis*). The estimates are considerably higher than the median rates calculated directly from the data. Two factors may have contributed to the difference. Firstly, negative increments were excluded from the simulated growth curves, but were included in the calculations from the data. Secondly, the maximum

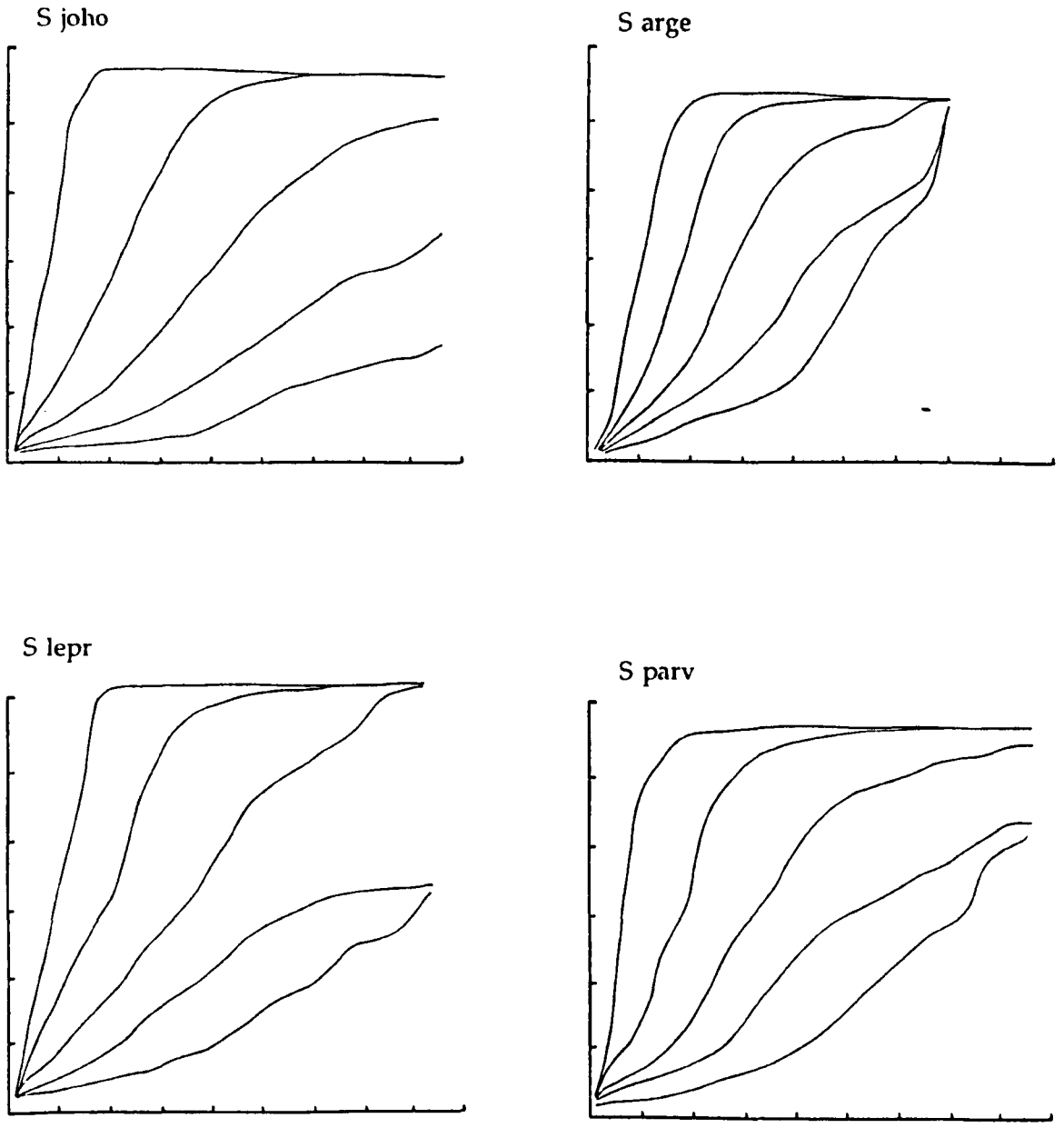


Figure 4.7 Simulated growth curves for different species in Plot 1. Height increments over the second interval were used to construct the curves (see text for details). Height intervals on *y*-axis are 100 cm; age intervals on *x*-axis are 10 years.

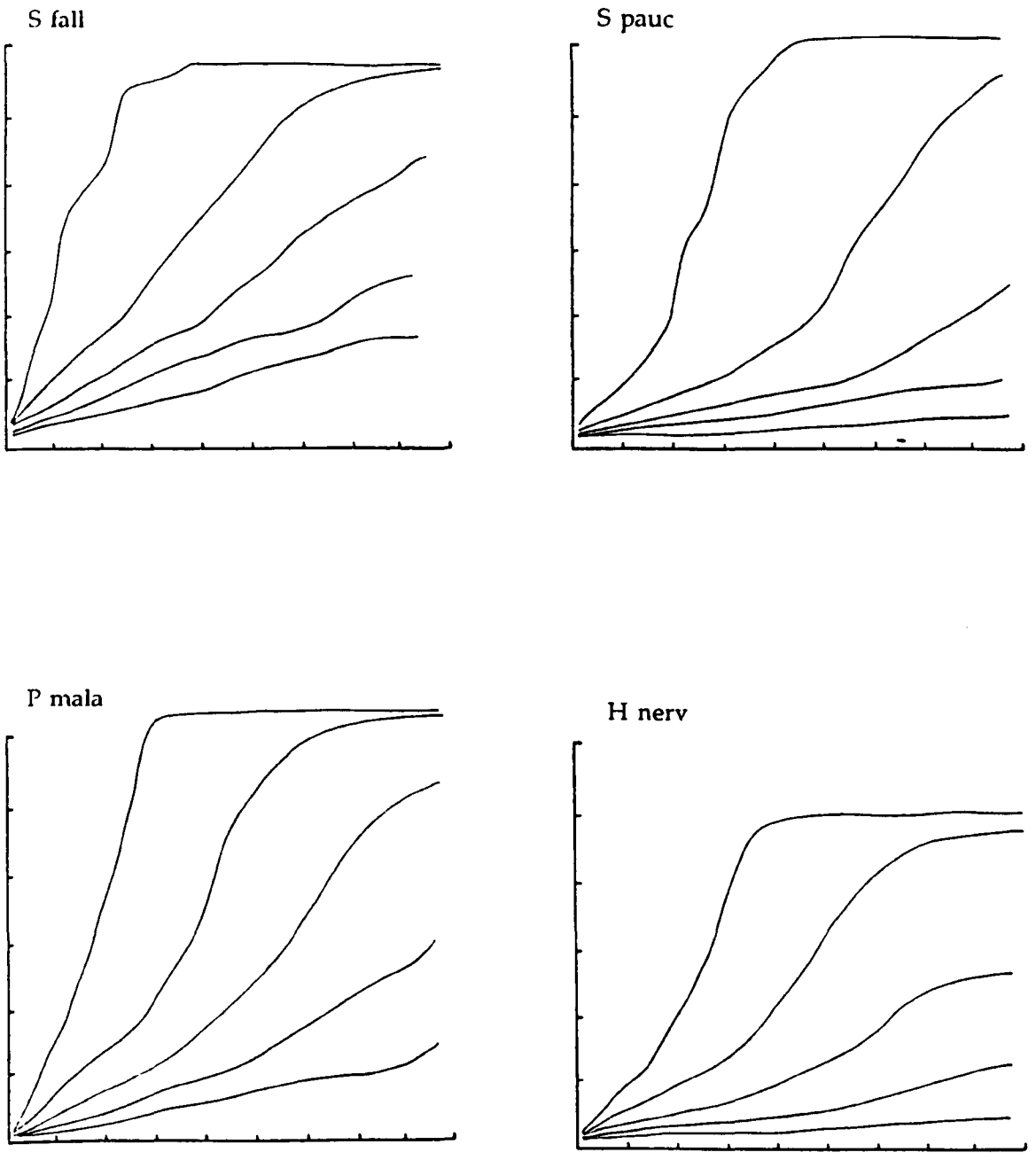


Figure 4.7 (continued) Simulated growth curves for different species in Plot 1. Height increments over the second interval were used to construct the curves (see text for details). Height intervals on y-axis are 100 cm; age intervals on x-axis are 10 years.

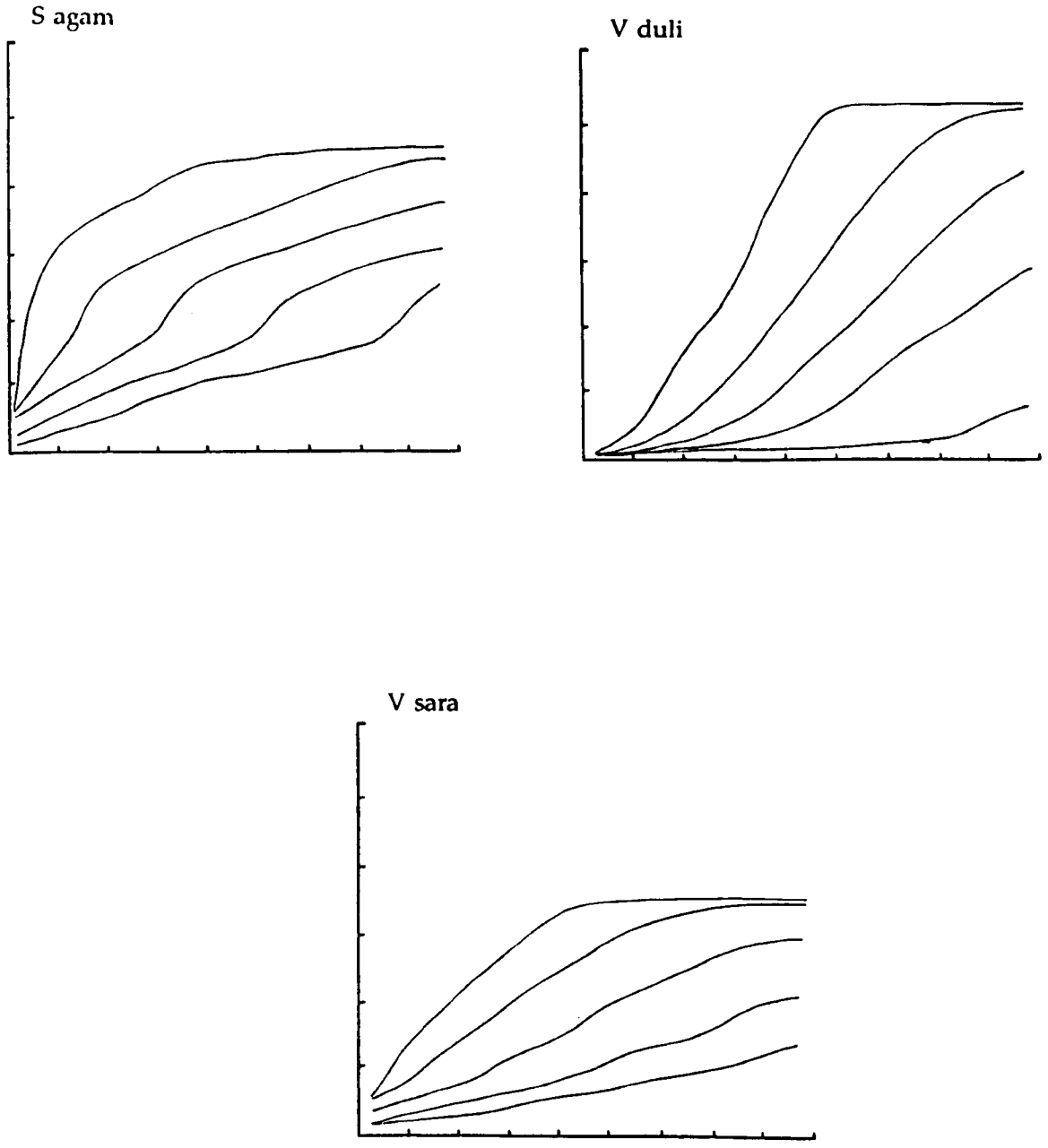


Figure 4.7 (continued) Simulated growth curves for different species in Plot 1. Height increments over the second interval were used to construct the curves (see text for details). Height intervals on y-axis are 100 cm; age intervals on x-axis are 10 years.

Table 4.6 Estimates of median, maximum and minimum growth rates (cm yr^{-1}) and estimated time to reach 5 m height derived from simulated growth curves (Fig. 4.8). Increments from second interval in Plot 1 were used.

Species	Estimates of growth rate (cm yr^{-1})			Minimum time (yr) to reach 5m tall
	median	maximum	minimum *	
S joho	7.89	52.5	2.64 0.99	11.0
S arge	14.73	36.3	12.13 2.42	15.9
S lepr	8.33	36.2	5.13 2.15	14.5
S parv	9.86	47.1	7.84 1.81	11.0
S fall	4.65	19.2	1.75	24.1
S pauc	6.97	16.5	0.52	31.7
P mala	6.44	27.4	1.98	24.8
H nerv	8.91	27.5	0.56	37.3
S agam	3.77	43.2	2.07	44.2 (4.5m) **
V duli	8.87	18.3	4.53	45.5
V sara	3.62	8.7	1.65	41.4 (3.5m) **

* upper figure is estimated minimum rate for larger seedlings and lower figure that for smaller seedlings (see Fig. 4.8)

** height of largest seedling: none reached 5m tall

rate on the simulated curves was often reached over a short range of heights, whereas the calculation from data included seedlings of all heights. In species with larger variation in size-specific growth rates, the discrepancy was greater.

Minimum rates were higher in the fast-growing species than in slow-growing species, suggesting that fast-growing species could not sustain low growth rates over time. The estimates of minimum growth rate ranged from 0.52 cm yr^{-1} in *S. pauciflora* to 12.1 cm yr^{-1} in *S. argentifolia* seedlings over 1 m tall. Minimum growth rates showed greater variation with size in fast-growing species, and increased with seedling size. The variation in minimum rate with size within these species was as great as the variation between species: between species (for seedlings less than 1 m tall), the highest minimum rate was 4.3 times the lowest; within *S. argentifolia*, minimum rate of seedlings > 1 m tall was 5.0 times the rate of smaller seedings. While the minimum growth rate must be sustainable over a few years, it is unlikely that a seedling could sustain such a slow rate of growth over tens of years. For this reason it was considered that estimates of seedling longevity based on the minimum trajectory were unlikely to be realistic, (compare estimates of tree longevity: Lieberman *et al.* 1985a) since mortality rates of seedlings are higher than those of trees, and most suppressed seedlings are more likely to die than to sustain very slow growth rates over many years.

The maximum rates of growth estimated from the simulated growth curves are lower than the maximum rates recorded in individual seedlings. While the fastest growing seedling in the data set is used in constructing the trajectories, this individual increment will be part of a trajectory which includes other, slower-growing, or suppressed, individuals. For the same reason, the estimates of time taken to reach 5 m height are likely to be over-estimated. Estimates ranged from 11 years in *S. johorensis* and *S. parvifolia* to over 40 years in *V. sarawakensis* and *S. agamii*. Maximum increments recorded in *S. johorensis* were over 1 m yr^{-1}.

4.12 DISCUSSION

Variation between individuals

There was very high variability in growth between individuals, even within the same species and size class. The frequency distributions of growth rates (Figure 4.1) emphasise this point. What are the causes and consequences of variation in growth rate? The high frequency of negative increments is immediately obvious - they formed a substantial proportion of the population in every species. The main cause of damage resulting in height loss was impact by falling trees and branches: the stem was broken, or bent over so that a lower accessory bud (Ng 1976, Chapter 2.6) developed as leading shoot. The other main cause of height loss was die-back, from pathogen or herbivore attack or for physiological reasons.

Physical damage from branch-falls is a well-documented cause of seedling mortality in tropical forests (see references in Chapter 3.7). Branch-falls have also been noted as a cause of height loss in surviving seedlings: Turner (1990) records stem breakage caused by falling branches in small seedlings in three species of *Shorea* in lowland dipterocarp forest in Penang. Clark & Clark (1992) report height losses of over 1 m in a year in saplings under 4 cm dbh, and 2.6-6.3 m in saplings 4-10 cm dbh in a tropical wet forest at La Selva, Costa Rica. Height losses of 2-4 m over 22 months were recorded in the Danum plots in seedlings less than 10 cm gbh (≈3 cm dbh). Die back, for undefined reasons, has been recorded in *S. leprosula* saplings growing in secondary forest (Wyatt-Smith 1958). Since branch falls are likely to occur randomly in space, each seedling should have an equal chance of being hit, independent of species. In contrast, die-back could be a species-specific response to damage caused by, for example, herbivory or water stress.

The differences observed between species in the numbers of individuals losing height may reflect differences in ability (or time taken) to regrow a lost apex and resume growth to recover the lost height, rather than differences in the frequency of damage. One would therefore expect fewer negative increments in fast-growing species which could quickly regrow, and more in slow-growing species, in which stem damage could accumulate faster than the seedlings can regrow. *H. nervosa*, a slow growing species, suffered more height loss than other species, not because this

species suffered more damage, but because its growth rate was too slow to recover the losses. This is supported by the observation that the number of *H. nervosa* seedlings in Plot 1 that lost height was greater over the combined interval than over each interval separately, suggesting that height loss accumulated faster than renewed growth could recover the lost height.

However, heavy damage was also particularly prevalent in seedlings 1-3 m tall in the LRMs and *S. johorensis* - fast growing species which should have been able to regrow rapidly enough to recover lost height. For example, over the first interval in Plot 1, 10% of *S. johorensis* seedlings lost a quarter or more of their main stem. It is possible that LRM seedlings over 1 m tall have reached that height because they were in a canopy opening, where damage by branch-falls is more likely (Aide 1987), while seedlings in more shade-tolerant species can grow to that height in the relative safety of closed forest.

A further source of variation in growth rates is dormancy, caused by the apical bud either resting or aborting at the end of each flush of growth (Ng 1981). In a survey at Madai FR in Sabah, Liew & Wong (1973) record 269/668 (40%) seedlings dormant over 1 year; no details of size or species composition are given. In the Danum, in Plot 1, 43%-45% of seedlings were dormant over each interval, and 35% in Plot 2. However, the definition of zero growth used in the Danum plots (Section 4.2) is almost certainly broader than that used by Liew & Wong, so the results are not comparable.

In Plot 1, frequency of dormancy was lower over the second interval (14 months) than over the first (5-6 months); for example, 25% of seedlings less than 50 cm height had no net growth over the first interval, compared with 10.4% over the second interval. Many seedlings that were dormant in the first interval appear to have resumed growth during the second interval. However, 7% of these small seedlings had no net growth over 22 months. It is also possible that growth was more difficult to detect over the first, shorter, interval in Plot 1, since height was measured to the nearest centimetre.

The combination of height loss and dormancy has a large effect the seedling growth in the population as a whole. Calculation of mean values demonstrated the impact of height loss and dormancy on the population. In the Danum plots, over 22

months, mean seedling growth rates were negative in two species. In Turner's (1990) study, height loss led to negative mean increments over 1 year in single cohorts of three *Shorea* species. Clark & Clark (1992) found that 13-37% of seedlings under 1 cm dbh had no net height growth in four years at La Selva, Costa Rica. In Plot 1, over 22 months, 57% of seedlings were in the damaged or zero growth categories.

Physical damage led to another source of variation in growth rates: seedlings regrowing after stem breakage could produce large increments. Presumably, if the root system was undamaged, it was large relative to the height of the broken stem, allowing rapid height recovery. A large proportion of seedlings showed scars from previous stem breakage (Chapter 2.4). The high frequency of damage by falling branches, breaking or bending over stems, emphasises the importance of the accessory buds described by Ng (1976) - could they have arisen in response to the need to recover from repeated damage?

Maximum growth rates

Examination of the maximum growth increments achieved by individual seedlings may reveal inherent differences in growth potential between species. Large growth increments were recorded in seedlings exposed to some degree of canopy opening - usually small partial gaps produced by either falls of small canopy or understorey trees, or branch-falls from large trees. These small openings increased the light available to seedlings, but were rarely complete gaps *sensu* Brokaw (1982).

Assuming that such openings occur randomly in space, the chance of encountering a gap would be similar for each individual, regardless of species. However, species differed in population size and spatial pattern, so that randomly-occurring canopy openings will interact with species dispersion patterns, resulting in differences between species in the likelihood of encountering an opening. The likelihood will be higher in abundant, well-dispersed species (*P. malaanonan*), and lower in less abundant species (*S. agamii*), and those with more clumped distributions (*V. dulitensis*, *S. fallax*). Highest maximum growth rates were found in the LRMs and *P. malaanonan*. Five species achieved maximum increments over 1 m yr^{-1}.

Maximum RGR was significantly correlated with median RGR: species with individuals attaining fast growth rates generally also had high median rates.

However, large individual increments could be produced by individuals in species with low median growth rates (eg. maximum increments in *H. nervosa* seedlings were 70-90 cm yr^{-1}).

In saplings 1-10 cm dbh at La Selva, Costa Rica, maximum height growth rates exceeded medians by an order of magnitude (Clark and Clark 1992). In the Danum plots, maximum growth rates were 10 to 100 times higher than medians. There was some evidence that the difference between maximum and median rates was less in both the fastest and slowest-growing species. In species with high maximum rates, median rates were also high: a large proportion of the population achieved fast growth rates. In species with low median rates, (eg. *V. sarawakensis* in Plot 1), the maximum rate tended to be low also. In species with intermediate median growth rates, individual seedlings could achieve maximum rates as high as in some of the fastest-growing species. Examination of the simulated growth curves confirms that variability in growth rates was higher in species with intermediate growth rates.

Variation between species

S. argentifolia had the highest median growth rates in both plots. *S. johorensis* seedlings could produce large increments (the largest recorded, 166 cm yr^{-1}, was in *S. johorensis*), but median growth rate was usually lower than the three LRMs. *P. malaanonan* seedlings also produced large individual increments (over 1 m yr^{-1} in both plots), but because there were large numbers of suppressed seedlings in the population, the medians were lower than the three LRMs.

The growth pattern of *S. fallax* differed in the two plots. In Plot 1 there was a high proportion of suppressed seedlings over 2 m tall, many with no clear leading shoot. The population in Plot 2 consisted mainly of seedlings less than 1 m tall growing in a light gap below the dead parent tree. These seedlings had high rates of growth: median AHI was higher than any other species, and RGR was second to *S. argentifolia*.

Looking at the percentage of seedlings in the fast-growth category (RGR>16 $\%yr^{-1}$) emphasises the high growth rates in *S. argentifolia*. Over 20% of individuals achieved fast growth rates (second interval, Plot 1), compared with less than 15% in other species. In *V. sarawakensis*, one of the slowest-growing species, 11% of seedlings

had fast growth rates, more than in *S. johorensis*. Slow growth rates were recorded in 40-50% of seedlings of LRMs, *S. johorensis* and *P. malaanonan*, compared to 20-30% in most other species. Frequency of zero growth was lowest in the LRMs, 20-30%, intermediate in *P. malaanonan* (40%), and highest in the remaining species, the DRMs, *H. nervosa* and *V. sarawakensis* (50-60%).

In the LRMs, a combination of fewer dormant seedlings and more achieving slow rates of growth (up to twice as many as in other species), as well as fast rates contribute to the high median growth rate. This outweighed the often higher frequencies of heavy damage in these species. Slow-growing species could have a relatively high proportion of fast-growing seedlings, and could produce individual large increments, but generally had more dormant, and fewer slow-growing seedlings. There were therefore differences in species growth rates, although variation due to external causes could be high. Chance factors contributed greatly to the high variability, both enhancing and decreasing growth rates.

Comparison of growth rates with other studies

Comparison of growth rates with those in other studies suffers from the same problem as the comparisons of mortality rates: variability is high, and details of the size and species composition, and environmental factors are rarely given.

Fox (1972) states that *S. argentifolia* seedlings grow faster in natural forest than other dipterocarp species. In the Danum plots, *S. argentifolia* had consistently the highest rates of median RGR and AHI, and in Plot 1, grew very significantly faster ($P<0.001$) than any other species. Liew & Wong (1973) report height increments for dipterocarp seedlings with a mean initial height of 76 cm, but unspecified species composition at Segaluid-Lokan, near Sandakan. In closed forest, mean AHI was 12.2 cm yr^{-1}, and 43.9 cm yr^{-1} in 'liberated forest'. In the same area, Nicholson (1965) recorded mean AHI of 1.2 cm yr^{-1}.

At Madai F.R. Liew & Wong (1973) report mean AHIs of 3.3 cm (range 2.5-7.6 cm) and 10.9 cm (2.5-40.6 cm) in dipterocarp seedlings in closed and 'lightly liberated' forest respectively. In logged forest at Kalabakan F.R., *S. parvifolia* seedlings grew faster than those of *S. leprosula* (61-101 cm yr^{-1}, compared to 30-58 cm yr^{-1}), and *S. johorensis* seedlings grew faster than both (64-122 cm yr^{-1}). In the Danum plots, *S.*

johorensis had consistently slower median growth rates than the other two species. Maximum rates recorded in the Danum plots are in the same range as these values, but median increments are lower, probably because of the high number of negative increments, which are usually excluded from other studies.

CHAPTER 5

RELATIONSHIPS BETWEEN GROWTH AND MORTALITY RATES

5.1 INTRODUCTION

Among populations of tropical tree species, adaptive or life-history trade-offs are expected between the ability to persist in the understorey (survival) and the ability to grow rapidly in response to canopy openings (Denslow 1980, 1987, Bazzaz 1984, Hubbell & Foster 1990). In addition, a correlation between mortality and growth rates across species would provide some evidence that equilibrating or stabilising forces may be regulating species populations and therefore contributing to the maintenance of high species diversity.

Two recent studies have demonstrated a positive correlation between mortality and growth rates across species in lowland tropical forest on Barro Colorado Island, Panama, in trees (Hubbell & Foster 1990) and in saplings 1-4 cm dbh (Welden et al. 1991). Both these studies included the range of species present in the forest from shade tolerant canopy trees to pioneer species.

The relationships between growth and mortality rates across species in the dipterocarp seedlings in Danum were investigated at two levels. At the population level, the correlation between growth and mortality rates across species was examined. The second approach used information on growth rates of individuals within species to examine the influence of growth rate on subsequent mortality in two ways. Firstly, rates of subsequent mortality in seedlings in different growth categories were compared. Secondly, previous growth rates were compared in seedlings which died versus survivors. Only data from Plot 1, where growth and mortality were recorded over two intervals, were used for these analyses.

5.2 METHODS

5.2.1 Relationships between growth and mortality across species

Correlations between species mortality rates (log annual rate) and growth rates (median RGR), within each plot, were tested with the Spearman rank correlation test. Species with fewer than 20 individuals in each plot were excluded (*S.* cf *symingtonii* in both plots and *Shorea* species 10 in Plot 1). The 1985 cohort of *V. dulitensis* seedlings was excluded from the Plot 1 analyses.

5.2.2 Relationships between growth and mortality within species

Seedlings were assigned to five growth categories according to their net growth rate during the first interval, as described in Chapter 4.2. Mortality in each category over the second interval was compared to test the null hypothesis that mortality did not differ significantly between growth categories, i.e. that seedlings with negative or zero increments during the first interval had the same probability of dying during the second interval as seedlings with positive growth. Contingency tables (5x2) of growth category versus status (dead or alive) at the third enumeration were tested with a χ^2 test (df=4). Where the expected number in any category was less than 1.0 (Snedecor & Cochran 1980), that category was pooled with an adjacent category. The seven species with more than five dead seedlings were tested separately and pooled. Light Red and Dark Red Merantis were compared. To investigate the changing relationship between growth and mortality with size, six height classes within the seven pooled species were compared.

In a second analysis, growth rates over the first interval were compared for seedlings that survived to the third enumeration and those that died. The Mann-Whitney U-test was used to test the null hypothesis that there was no difference in previous median growth, both absolute and relative rate, between the two groups. Previous growth rate was compared for seedlings in the seven major species, all species pooled. A further test compared all seven species pooled in six height classes.

5.3 RESULTS

5.3.1 Relationships between growth and mortality across species

The ranking of species growth and mortality rates within each plot, and Spearman rank correlation coefficients are given in Table 5.1. The relationship between species mortality rates and median annual growth rates in the two plots is shown in Figure 5.1.

Growth and mortality rates were generally positively correlated. Species with fast growth rates tended to have high mortality rates. In Plot 1, species mortality rates during the second interval were significantly correlated with median growth rates over both the second and combined intervals (Table 5.1). Mortality and median growth rates were not correlated over the first interval ($P>0.05$). *S. argentifolia* had the fastest growth rate and the highest mortality over all intervals. Low rates of both growth and mortality were found in *H. nervosa* and *V. sarawakensis*. Behaviour of other species was less consistent. For example, *S. parvifolia* was ranked seventh for growth rate, but third in mortality rate over the first interval, then second in growth rate and fifth in mortality over the second interval. In this species, median growth rate was significantly higher over the second interval, while there was no difference in mortality rate (Table 5.1). The greatest differences in ranking over the combined interval were in *S. johorensis* (second highest mortality but ranked fourth in growth rate) and *S. pauciflora* (third highest mortality, ninth in growth), while *S. parvifolia* was ranked lower for mortality (fifth) than for growth (second).

In Plot 2 there was no significant correlation between species median growth and mortality rates (Table 5.1). Much of the difference in rank was accounted for by three species. *S. fallax* had the second highest growth rate, but was ranked seventh for mortality rate. *P. malaanonan* had the third highest mortality, combined with sixth ranked growth rate, and *S. johorensis* was ranked eighth in growth but fifth in mortality.

The range of growth and mortality rates was similar in the two plots. Two species were outliers, both in Plot 2: *S. fallax* and *S. argentifolia* had higher growth rates relative to their mortality rates than other species.

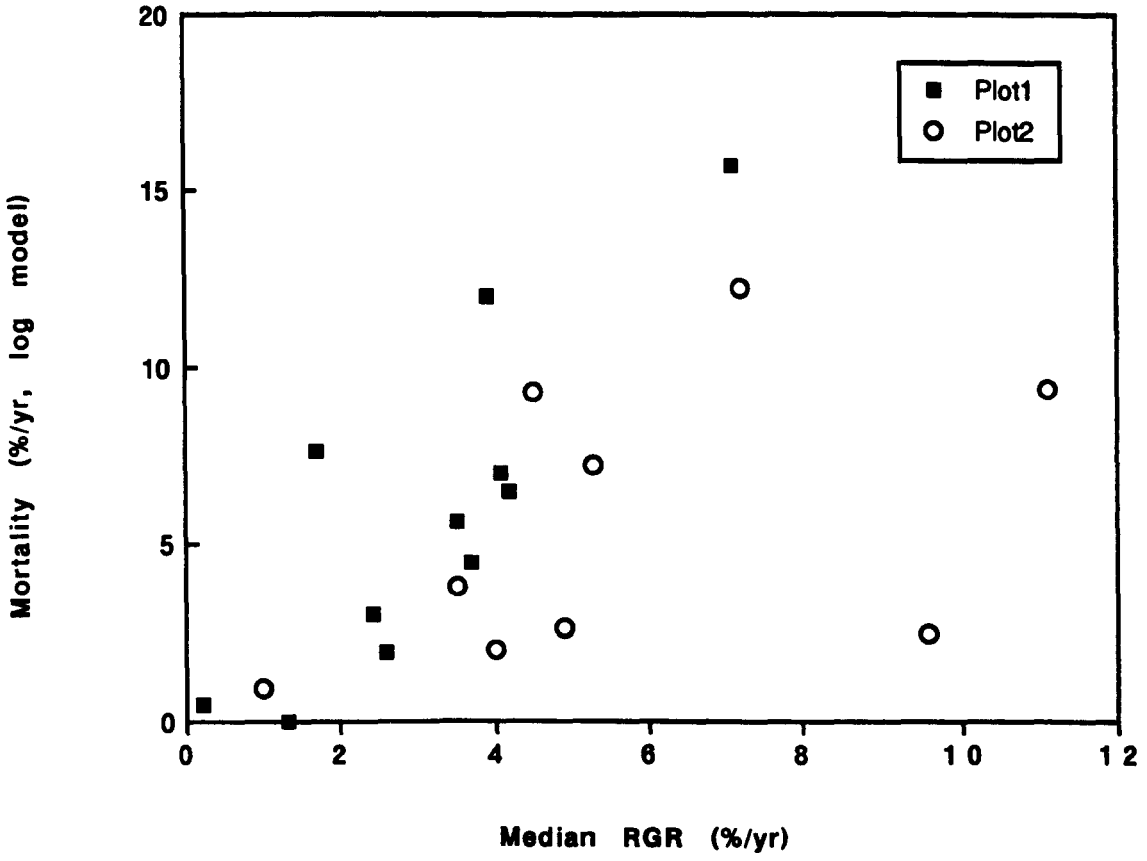


Figure 5.1 Relationship between rates of mortality (% yr^{-1}, log model) and median growth (Relative Growth Rate, RGR, % yr^{-1}) in different species in Plots 1 and 2.

Table 5.1 Rank order of species median Relative Growth Rates (RGR, % yr^{-1}), and mortality rates (m, % yr^{-1}, log model). Spearman rank correlation co-efficients (r_s) for the relationship between species growth and mortality rates within each interval are given.

	Plot 1						Plot 2	
	Interval							
	first		second		combined			
Species	RGR	m	RGR	m	RGR	m	RGR	m
S joho	5	4	5	2	4	2	8	5
S arge	1	1	1	1	1	1	1	2
S lepr	2	7	3	3	3	4	4	4
S parv	7	3	2	5	2	5	3	1
S fall	8	8	7	8	8	8	2	7
S pauc	6	2	10	4	9	3	-	-
P mala	4	6	4	7	5	7	6	3
H nerv	9=	9=	11	10	11	10	7	8
S agam	3	9=	8	9	7	9	-	-
V sara	9=	9=	9	11	10	11	9	9
S pilo	-	-	-	-	-	-	5	6
V duli	9=	5	6	6	6	6	-	-
r_s	0.723		0.339		0.682		0.583	
P	*		N.S.		*		N.S.	

5.3.2 Relationships between growth and mortality within species

Growth category and mortality: variation between species and species groups

Numbers of dead seedlings and survivors, and percentage mortality for each species in the five growth categories are given in Table 5.2. For all species pooled, differences in subsequent mortality between growth categories were not statistically significant overall (Table 5.2). Mortality was highest in the heavy-damage category, 12.2%, and decreased to 8.6 - 8.8% in seedlings with zero and positive increments.

Within each species, differences between growth categories in numbers of seedlings which subsequently died were not statistically significant (χ^2 test, $p>0.05$), except in *S. fallax*. However, highest mortality occurred in one of the negative growth categories in six of the seven species (Table 5.2). The probability of this occurring is $(2/5)^6 = 0.004$. Mortality in the heavy-damage category was almost five times higher than in the fast growth category in *P. malaanonan*, and around double in *S. johorensis* and *S. parvifolia*.

Differences in subsequent mortality between the growth categories in each Meranti group were not significant. In the DRMs, mortality decreased with increasing previous growth performance, while the trend was less clear in the LRMs (Figure 5.2). Highest mortality rates were in the moderate-damage category in the LRMs, and in the heavy-damage category in DRMs. Lowest mortality was in the slow-growth category in LRMs and in the fast-growth category in DRMs.

Growth category and mortality: variation with size

Numbers of seedlings which subsequently died, and percentage mortality, in the five growth categories for six height classes in seven species pooled are given in Table 5.3. There were no significant differences in mortality between growth category in any height class. However, the risks of subsequent mortality in different growth categories showed differing trends with increasing size. In seedlings with low negative, zero and low positive increments, the risk of subsequent death decreased with increasing height. For fast-growing seedlings, and those that had suffered heavy damage, the risk of mortality tended to increase with size. In the smallest seedlings (≤50 cm height), fast-growing seedlings had the lowest mortality, while in the largest saplings, fast-growing seedlings had the highest mortality.

Table 5.2 Numbers of seedlings dead (D) and alive (A) at the third enumeration (Plot 1), and mortality rate (total %) in five growth categories (defined in Chapter 4.2) for seven species, Light Red Merantis (LRM) with *S. johorensis* and Dark Red Merantis (DRM) in Plot 1. Probability values, P, are from a χ^2 test of the contingency table in each species.

	Growth category													
	- -		-		≈ 0		+		+ +		Total %			
Species	D	A	D	A	D	A	D	A	D	A	D	A	P	
S joho	4	10	6	19	20	105	11	66	5	28	46	228	N.S.	
	(28.6)		(24.0)		(16.0)		(14.3)		(15.2)		(16.8)			
S arge	1	6	5	9	15	37	12	56	9	38	42	146	N.S.	
	(14.3)		(35.7)		(28.8)		(17.6)		(19.1)		(22.3)			
S lepr	1	12	0	7	7	42	3	50	3	18	14	129	N.S.	
	(7.7)		(0.0)		(14.3)		(5.7)		(14.3)		(9.8)			
S parv	3	13	1	17	2	75	7	41	1	11	14	157	N.S.	
	(18.8)		(5.6)		(2.6)		(14.6)		(8.3)		(8.2)			
S fall	5	39	0	50	9	239	6	135	0	36	20	499	*	
	(11.4)		(0.0)		(3.6)		(4.3)		(0.0)		(3.9)			
S pauc	2	31	7	36	20	185	12	122	2	43	43	417	N.S.	
	(6.1)		(16.3)		(9.8)		(9.0)		(4.4)		(9.3)			
P mala	3	26	2	48	10	205	9	165	1	47	25	491	N.S.	
	(10.3)		(4.0)		(4.7)		(5.2)		(2.1)		(4.8)			
LRM + S joho	9	41	12	52	44	259	33	213	18	95	116	660	N.S.	
	(18.0)		(18.7)		(14.5)		(13.4)		(15.9)		(16.4)			
DRM	7	70	7	86	29	424	18	257	2	79	63	916	N.S.	
	(9.1)		(7.5)		(6.4)		(6.5)		(2.5)		(6.4)			
Total	19	137	21	186	84	888	60	635	21	221	204	2067	N.S.	
	(12.2)		(10.1)		(8.6)		(8.6)		(8.7)		(9.0)			

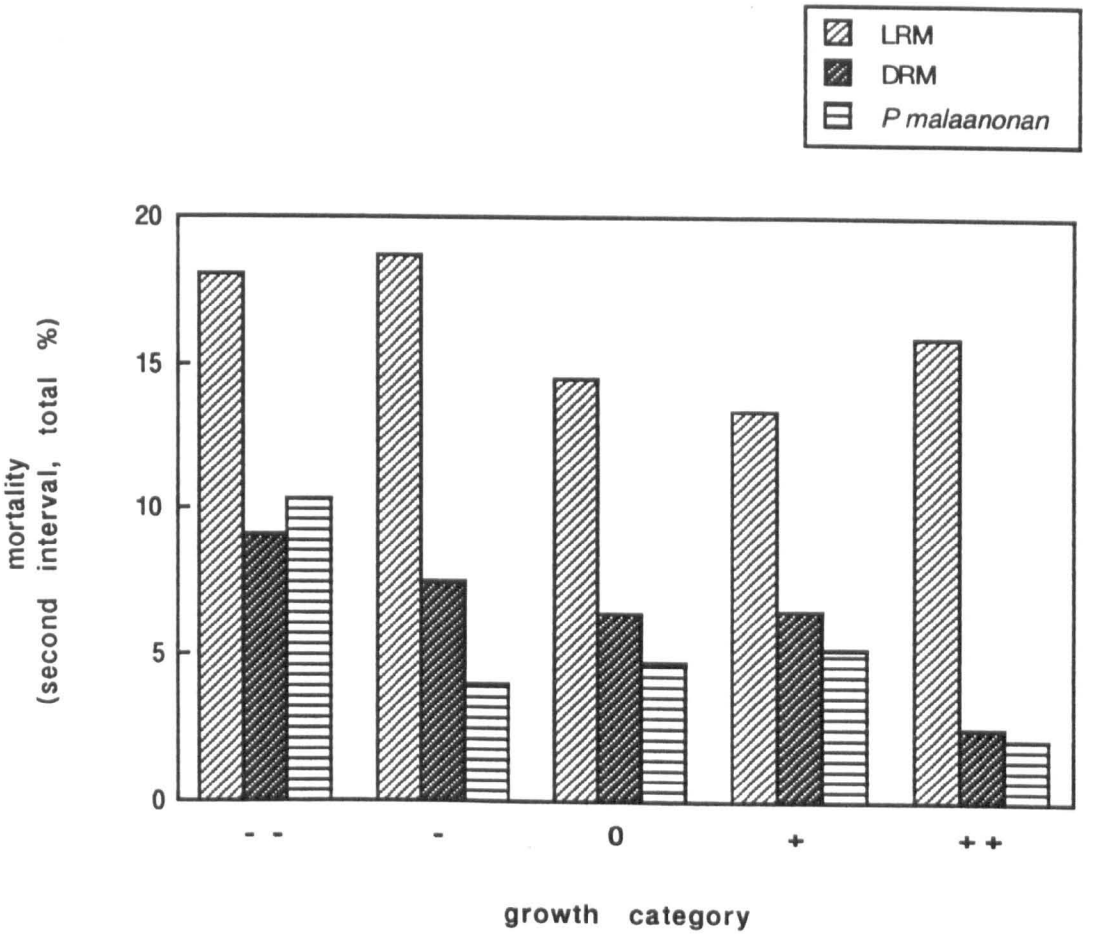


Figure 5.2 Mortality rate over the second interval in relation to previous growth category in Light and Dark Red Merantis (LRM, DRM) and in *Parashorea malaanonan* in Plot 1 (see Section 4.2 for definition of growth categories).

Table 5.3 Numbers of seedlings dead (D) and alive (A) at the third enumeration (Plot 1), and mortality rate (total %) in five growth categories (defined in CHapter 4.2) in six height classes for individuals in seven species (same species as Table 5.2) pooled. Probability values, P, are from a χ^2 test of the contingency table in each height class.

	Growth category						
Height class (cm)	- -	-	≈0	+	+ +	Total %	
	D A	D A	D A	D A	D A	D A	P
> 50	3 18 (14.3)	8 44 (15.4)	19 98 (16.2)	25 126 (25.0)	6 74 (7.5)	61 360 (14.5)	N.S.
51 - 100	6 45 (11.8)	11 56 (16.4)	35 306 (10.3)	24 243 (9.0)	7 74 (8.6)	83 724 (10.3)	N.S.
101 - 150	1 24 (4.0)	0 27 (0.0)	9 208 (4.1)	7 130 (5.1)	2 29 (6.5)	19 418 (4.3)	N.S.
151 - 200	3 17 (15.0)	1 27 (3.6)	10 97 (9.3)	3 54 (5.3)	4 24 (14.3)	21 219 (8.7)	N.S.
> 200	6 33 (15.4)	1 32 (3.0)	10 179 (5.3)	1 82 (1.2)	2 20 (9.1)	20 346 (5.5)	N.S.
Total	19 137 (12.2)	21 186 (10.1)	83 888 (8.6)	60 635 (8.6)	21 221 (8.7)	204 2067 (9.0)	N.S.

Previous growth rate and mortality: variation between species and size classes

Median RGRs and AHIs for survivors and dead seedlings are given in Table 5.4 (grouped by species) and Table 5.5 (grouped by height class). For the seven species pooled, AHI was significantly lower in seedlings that died, but RGRs did not differ. There were no significant differences in previous RGR between survivors and dead seedlings in any species. Dead seedlings had significantly lower AHI previously in two species, *S. johorensis* and *S. argentifolia* (Table 5.4), and differences in AHI approached significance in *P. malaanonan* (P=0.057). Previous growth rates, both RGRs and AHIs, were consistently lower in seedlings which died than in survivors in all species except *S. parvifolia*.

For all seven species pooled, differences in median previous RGR and AHI were not significant in any height class, except for AHI in the largest saplings, over 300 cm tall (Table 5.5). However, median AHI and RGR were lower in seedlings which died than in survivors in all height classes except the 101-150 cm class.

5.3.3 Size-related variation in growth and mortality

If there are size classes in which mortality is high, but growth low, then because more time is spent in that height class, the risk of mortality is magnified. Conversely, size classes with the combination of high growth rates and low mortality rates may enhance performance.

Variation with height class in rates of mortality and growth is illustrated in Figure 5.3. High mortality and low growth rates occurred in small seedlings in all the emergent *Shorea* species except *S. fallax*. In larger seedlings, the same combination was found in large *S. johorensis* (>150 cm), large *S. parvifolia* (>300 cm) and in *S. argentifolia* seedlings up to 200 cm tall. The alternative combination, high RGR and low mortality occurred in medium and large LRM seedlings, especially in *S. johorensis* seedlings 101-150 cm tall and *S. parvifolia* seedlings 101-200 cm tall. In small seedlings, low mortality and high RGR occurred in *S. fallax* and *P. malaanonan*.

Table 5.4 Comparison of median growth rates in the first interval (Relative Growth Rate, % yr^{-1}; and Annual Height Increment, AHI, cm yr^{-1}) between seedlings which later died and survivors at the third enumeration in seven species, Light Red Merantis (LRM) with *S. johorensis*, and Dark Red Merantis (DRM) in Plot 1. Mann-Whitney U-test was used to compare the two groups.

	Dead			Alive			P	
Species	N	RGR1	AHI1	N	RGR1	AHI1	RGR1	AHI1
S joho	46	2.48	1.86	228	2.58	2.48	N.S.	*
S arge	42	4.09	1.93	146	8.17	5.78	N.S.	*
S lepr	14	2.71	2.26	129	4.22	4.73	N.S.	N.S.
S parv	14	4.85	2.48	157	0.83	1.86	N.S.	N.S.
S fall	20	0.00	0.00	499	1.15	2.26	N.S.	N.S.
S pauc	43	0.00	0.00	417	2.28	1.86	N.S.	N.S.
P mala	25	1.84	1.86	491	2.80	1.93	N.S.	N.S.
LRM + S joho	116	2.85	1.93	660	3.51	3.71	N.S.	*
DRM	63	0.00	0.00	916	1.69	1.93	N.S.	N.S.
Total	204	1.89	1.86	2067	2.48	2.08	N.S.	*

Table 5.5 Comparison of median growth rates in the first interval (Relative Growth Rate, % yr^{-1}; and Annual Height Increment, AHI, cm yr^{-1}) between seedlings which later died and survivors at the third enumeration in seven species (Table 5.4) in six height classes in Plot 1. Mann-Whitney U-test was used to compare the two groups.

	Dead			Alive			P	
Height class (cm)	N	RGR1	AHI1	N	RGR1	AHI1	RGR1	AHI1
1 - 50	61	4.20	1.86	360	4.88	1.93	N.S.	N.S.
51 - 100	83	3.03	1.93	724	3.02	2.26	N.S.	N.S.
101 - 150	19	3.38	4.73	418	1.97	2.48	N.S.	N.S.
151 - 200	21	0.00	0.00	219	1.48	2.48	N.S.	N.S.
201 - 300	16	-1.10	-2.42	222	0.81	1.93	N.S.	N.S.
> 300	4	-140.07	-393.39	124	0.00	0.00	N.S.	*
Total	204	1.89	1.86	2067	2.48	2.08	N.S.	*

The three LRMs had similar patterns of changing growth and mortality with size class. All three had high rates of both mortality and growth (RGR) in small size classes. Both growth and mortality reached a second peak in medium-sized seedlings (Figure 5.3). The two DRMs differed from each other in size-related growth and mortality. In *S. pauciflora*, mortality decreased with increasing size, but RGR remained similar in all height classes. In contrast, mortality in *S. fallax* was constant with size, but RGR increased in smaller seedlings, paralleling the LRM pattern of growth (but growth in *S. fallax* did not increase again in larger seedlings). *P. malaanonan* had a similar patterns of both mortality and growth to *S. fallax*, although the overall rates of both were higher in *P. malaanonan*.

Performance may vary in this way on the population level too - for example, in both plots, *S. johorensis* was ranked lower for growth rate and higher for mortality relative to other species.

5.3.4 Relationships between mortality and growth rates and population size.

The observed differences in seedling growth and mortality rates might have an effect on population size. Numbers of seedlings in species with high mortality rates, for example the Light Red Merantis, are known to fluctuate over time (Fox 1972). In contrast, species with low mortality rates may accumulate seedling numbers over time, leading to high population size, or conversely, low mortality rates may be found in species with few seedlings. At Kade, Ghana, there were differences between two upper canopy species (*Celtis* and *Strombosia*) in adult and seedling abundance and seedling mortality rates, leading Swaine (1989) to suggest that the adult population can be maintained in *Celtis*, despite low seedling density, because of the low mortality rate, while because of the higher juvenile mortality in *Strombosia*, a higher number of seedlings is required to maintain adult numbers.

Mortality rates and median RGRs (over the combined interval) for eleven species in Plot 1 are plotted against population size at the first enumeration (Figure 5.4). The eleven species fall into three non-overlapping groups: 1) species with low to intermediate numbers of seedlings, and high rates of growth and mortality; 2) species with large seedling populations, low growth rates and low mortality, and 3)

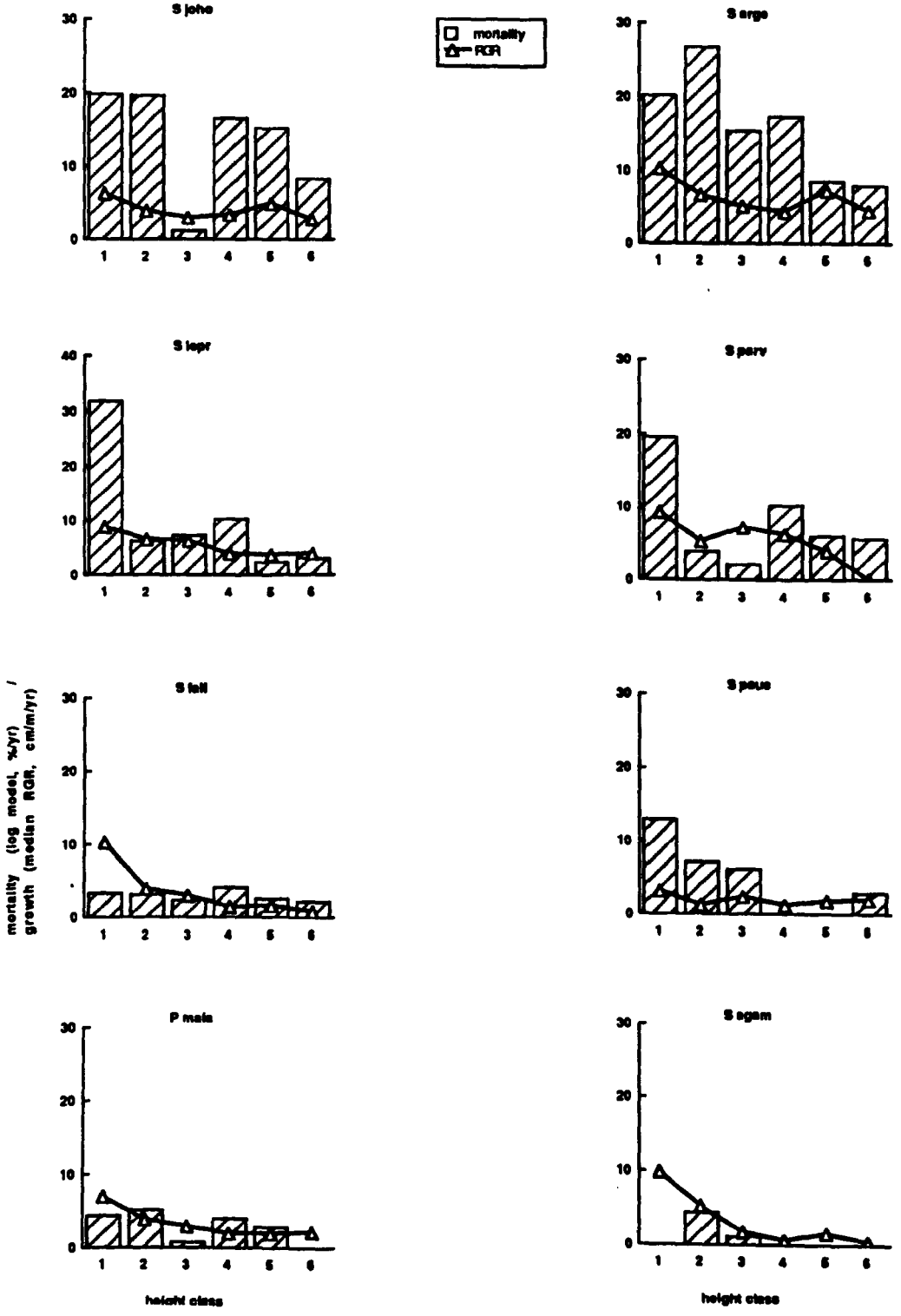


Figure 5.3 Relationship between rates of mortality (log model, % yr^{-1}) and growth (median Relative Growth Rate, RGR, % yr^{-1}) in six height classes, Plot 1, second interval. Height classes 1 to 4 are in 50 cm intervals; class 5, 201-300 cm; class 6, >300 cm.

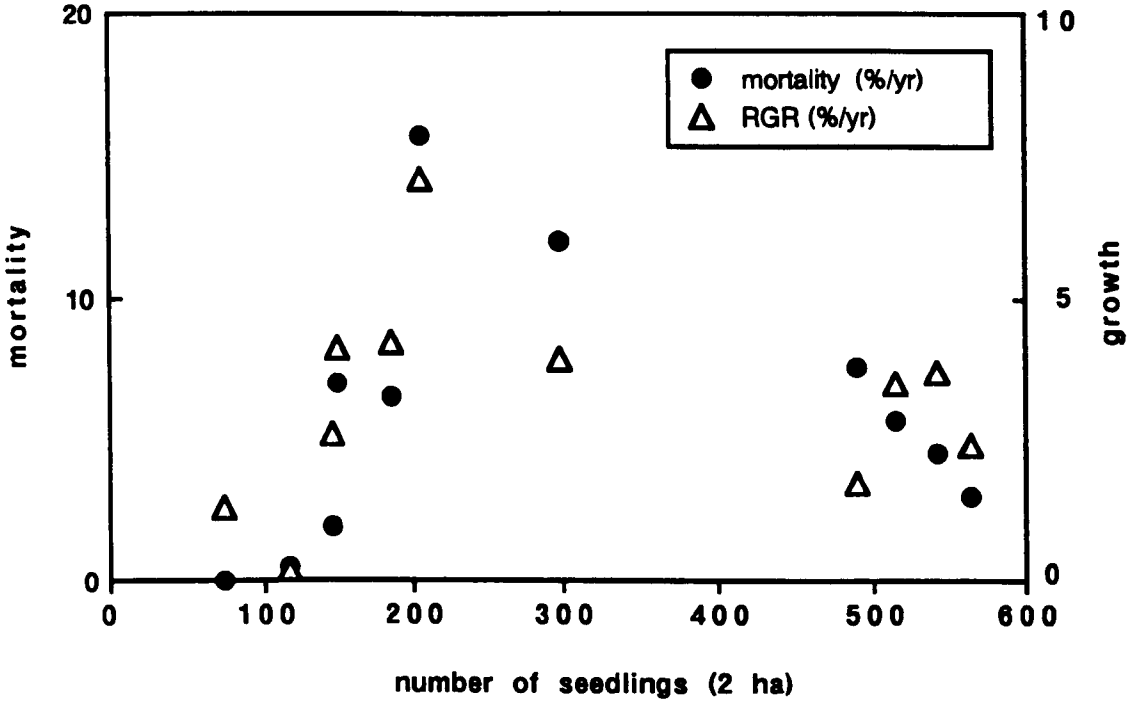


Figure 5.4 Relationship between population size, and rates of mortality (log model, % yr^{-1}) and growth (median Relative Growth Rate, RGR, % yr^{-1}) over the total interval in different species in Plot 1.

species with small seedling populations, low growth and mortality rates.

Group 1 comprises *S. johorensis* and the Light Red Merantis: *S. argentifolia*, *S. leprosula* and *S. parvifolia*, all emergent species. Group 2 includes the Dark Red Merantis: *S. fallax* and *S. pauciflora*, and *P. malaanonan*, also emergent species. The remainder, in Group 3, are all small, non-emergent species: *H. nervosa*,*V. sarawakensis* and *S. agamii*.

5.4 DISCUSSION

Population level correlations

Seedling mortality and median growth rates were positively correlated over the second and combined intervals in Plot 1. In Plot 2, the correlation was not significant. Correlation between growth and mortality rates demonstrates an expected trade off in tropical trees that are specialised for different light environments (Hubbell & Foster 1990). Positive correlation between mortality and growth has been recorded across species in a 50 ha plot of lowland tropical forest on Barro Colorado Island, Panama, in trees (Hubbell & Foster 1990) and saplings 1 - 4 cm dbh (Welden *et al.* 1991). Both these studies include species from the whole community of trees in the study plot, ranging from pioneer species to shade tolerant canopy trees. The present study demonstrated a significant correlation between growth and mortality rates of seedlings (<10 cm gbh or 3.2 cm dbh) in relatively few species within one family.

Growth and mortality rates were not significantly correlated in Plot 2, but the range of values was similar to that within Plot 1 (Figure 5.2). The species accounting for much of the difference in rank in Plot 2 was *S. fallax*, which had a high growth rate relative to both the mortality rate in Plot 2, and growth rate of the same species in Plot 1. An explanation for the differences in ranking of growth and mortality rates of *S. fallax* seedlings in Plot 2 may lie in the spatial distribution: the majority of seedlings were in a single clump in a light gap created by the death of a large canopy tree (the parent tree), and grew vigorously during the study, with low mortality.

Correlation of growth and mortality rates in Plot 1 during the first interval, *ca.* five months, was not significant, whereas it was over the second interval, *ca.* 18

months. The fact that the value of the correlation coefficient increased with length of interval in Plot 1 (Table 5.1) may suggest that short-term fluctuations in growth or mortality rate within a species tend to balance out in the longer term. For example, the differences in rank of growth and mortality in *S. leprosula*, *S. parvifolia* and *S. agamii* over the first interval were not maintained over the second interval. However, in *S. pauciflora* difference in rank was maintained: this species had a combination of low median growth rates and high mortality over both intervals.

S. johorensis in both plots was ranked lower for growth than for mortality. In both plots, it was the dominant tree species in terms of basal area. *S. pauciflora* was the second most abundant tree in Plot 1, and its seedlings had relatively lower growth than mortality. Similarly, in the second most abundant species in Plot 2, *S. parvifolia*, seedlings were ranked third in growth, but had the highest mortality. Thus, in both plots, seedlings of the dominant tree species had relatively poorer growth and higher mortality rates than other species. This may provide some support for the existence of the compensatory mechanisms proposed by Connell *et al* (1984): common species are predicted to have higher rates of mortality and / or lower growth than rarer species.

Mortality in relation to previous growth rate

Differences between growth categories in subsequent mortality were not significant in any species except *S. fallax*, nor in the two Meranti groups. In most comparisons however, subsequent mortality was higher in one of the negative growth categories.

Subsequent mortality did not differ between growth categories in six height classes. The trends in subsequent mortality with growth category varied between large and small seedlings. In small seedlings, fast-growing seedlings had less than half the mortality rate of all other categories. In larger seedlings, mortality became more concentrated in the fast growing and heavy-damage categories. Most of the deaths of fast-growing seedlings were in the Light Red Merantis and *S. johorensis*.

Higher mortality in suppressed trees over 30 cm gbh was recorded in moist semi-deciduous forest in Ghana (Swaine *et al.* 1987). Manokaran (1988) found that mortality was 7-8 times greater in suppressed trees than in growing trees (≥10 cm

gbh) in lowland dipterocarp forest in Malaysia.

Comparison of previous growth rate in seedlings which died and survivors gave a similar picture to the comparison of mortality between growth categories: differences were usually not statistically significant within species, or size classes, but in most comparisons, surviving seedlings had higher median growth in the previous interval.

Previous median height growth was significantly less in seedlings which died while median relative growth rate was not, for all species pooled, and within two species. This suggests that absolute height gain may be more important in terms of survival than relative growth. Previous height increment differed significantly in two fast-growing species (*S. argentifolia* and *S. johorensis*), suggesting that these species may be less tolerant of height loss or periods of slow growth.

In general, seedlings with low growth rates were less likely to survive than those with high rates of growth. While the differences were not statistically significant in most species, they were consistent, and may be biologically meaningful. Possibly the study period was too short for significant differences to be detected. Welden *et al.* (1991) found few differences in a comparison of sapling performance under differing canopy heights on BCI. They suggest that their three year study period may have been too short for differences in growth and mortality responses to be detected. In the present study, it is more likely that the enumerations were too far apart to detect a close link between poor performance and mortality: a seedling suffering die-back or stem breakage and dying within a few weeks would not necessarily have been detected in the surveys.

Comparison of Meranti groups

Comparison of subsequent mortality in growth categories in the two Meranti groups showed no significant differences within each group. The DRMs had a consistent trend of decreasing mortality with improving previous growth performance, while no such trend was evident in the LRMs. Rate of mortality varied more between categories in DRMs than in the LRMs - in DRMs, the highest mortality rate in any category was 3.6 times the lowest rate, compared with 1.4 times in the LRMs. This suggests that mortality in the LRMs was less closely related to previous

performance than is the case in DRMs. But this was contradicted by the comparison of previous growth rate in dead seedlings versus survivors: seedlings which survived had significantly higher absolute height growth previously than those which died in two species of LRM, and in the group as a whole. There were no differences in previous growth rate in DRMs.

Growth and mortality relationships in Light Red Merantis

Fast-growing LRM seedlings experienced a relatively high mortality rate (Figure 5.9). Both mortality and growth rates peaked in medium-sized LRM seedlings (Figure 5.8). Large height losses were more frequent in medium sized seedlings (Figure 4.2). Are these observations related? The conditions which lead to high growth rates in LRM saplings, canopy opening, may also bring the risk of physical damage from branch falls (Aide 1987), which are more likely in canopy openings than in mature forest (Hubbell & Foster 1986b, Welden *et al.* 1991). Many of the canopy openings in the Danum were caused by branch-falls, rather than tree-falls, and were small. They could be quickly filled by lateral branch growth from established trees (Denslow 1987). This brings a further risk to seedlings in these gaps: a seedling which has put on a rapid spurt of growth in response to the new canopy opening may find the available light quickly becomes too low to maintain the new growth.

Evidence from the simulated growth curves (Chapter 4.11, Figure 4.7) supports this idea. In the LRMs and *P. malaanonan*, the minimum growth trajectories of larger seedlings (usually over 100-150 cm tall) are faster than the minimum trajectory of smaller seedlings in the same species. In other species, the minimum rate remains more constant with increasing height. This suggests that slower-growing species can maintain slow growth-rates in all height classes, but saplings of light demanding species are unable to maintain slow growth rates beyond a critical size - they reach an 'all-or-nothing' stage.

Relationship between population size and rates of mortality and growth

Species in Plot 1 could be divided into three non-overlapping groups based

on their growth and mortality rates, and population sizes (Figure 5.4). Group 1 contained four emergent Red and Light Red Meranti species, with high rates of growth and mortality, and intermediate population sizes. These were common as emergent trees in the area, and are light-demanding, with timber classified as light hardwood (Burgess 1966). Group 2 contained the two Dark Red Meranti species and *P. malaanonan*, with lower rates of both growth and mortality. These are more shade tolerant species. The DRMs are classified as heavy hardwood, and *P. malaanonan* as light hardwood. In Group 3 were the slow-growing canopy species with low rates of growth and mortality: *H. nervosa*, *V. sarawakensis* together with *S. agamii*. These species have heavier timber than the species in the other two groups, but are usually too small and scarce to be of commercial value (Meijer & Wood 1964).

The large numbers of seedlings of the group 2 species (*S. fallax*, *S. pauciflora* and *P. malaanonan*) may be related, not to higher fecundity, but to the ability of the seedlings to survive for long periods in a suppressed state in the low light conditions of the forest floor, forming a large seedling bank (Meijer & Woods 1964, Whitmore 1984). Seedlings of the more light-demanding Light Red Merantis (group 1) lack the ability to remain suppressed for so long, and had higher mortality rates. The seedling bank in these species decreases more quickly between mast years (Fox 1972), despite high fecundity, and numbers fluctuate more than in other species.

CHAPTER 6

GROWTH AND MORTALITY RATES OF DIPTEROCARP TREES

Rates of mortality and growth for dipterocarp trees (≥10 cm gbh) are briefly described in this chapter to allow comparison with the seedling data, and to provide a fuller picture of the dynamics of dipterocarp populations within the plots; they are not discussed in detail. Individual species in each plot are included if their seedlings were present in the seedling study areas within the same plot. However, the overall mortality rates given include all dipterocarp trees within each plot.

6.1 TREE MORTALITY

To limit bias in the calculation of mortality rates introduced by differences in enumeration date, an average date was calculated as described in Chapter 3.1, this time to the nearest 0.25 month. Mortality rates for trees in Plot 2 relate to the period from December 1986 to July 1988, and in Plot 1 for the period between August 1985-February 1986 and July 1988. Annual mortality rates (log model) and estimated population half-lives for the interval between first enumeration and July 1988 are given in Table 6.1.

6.1.1 Overall mortality rates

In Plot 1, 49 out of 702 dipterocarps died between first enumeration and July 1988, and 37 out of 970 in Plot 2. Overall mortality rate for all dipterocarps was

2.75% yr^{-1} in Plot 1 and 2.42% yr^{-1} in Plot 2, giving estimated half-lives of 25.2 years and 28.6 years respectively. Of the dead trees in Plot 1, three had fallen, four appeared to have been killed by tree falls, five had disappeared without trace, and the rest were still standing.

Numbers dying between enumerations could not be compared between plots directly with a χ^2 test because the length of interval differed between plots. Instead, the mortality rate from Plot 2 was used to predict the number expected to die over the Plot 1 interval, given the mortality rate in Plot 2. This expected value was compared with the actual value with a χ^2 goodness-of-fit test. Mortality did not differ significantly between the plots (χ^2 =0.95, df=1, P>0.5).

6.1.2 Variation between species and size classes

In Plot 1, highest mortality rates were in the three Light Red Merantis, with annual rates ranging from 3.33% in *S. leprosula* to 5.13% in *S. parvifolia*, giving estimated half-lives of between 14 and 21 years. Overall mortality rate in LRMs was 4.57% yr^{-1}, giving an estimated $t_{0.5}$ of 15.2 years. Mortality of DRMs was similar to that of LRMs (χ^2 =3.72, df=1, P>0.05).

In Plot 2 mortality was highest in *S. johorensis* (6.84% yr^{-1}), followed by *S. argentifolia* (5.67% yr^{-1}). The other LRMs had lower mortality: 1.76% yr^{-1} in *S. parvifolia*, and no trees of *S. leprosula* died (but the population size was small). Mortality was also high in *H. nervosa*: 5.61% yr^{-1}. Mortality of LRMs was 2.67% yr^{-1} (estimated $t_{0.5}$: 26.0 yr), significantly lower than in Plot 1 (12 deaths were predicted from the Plot 2 mortality rate, over the time interval in Plot 1, compared to 20 observed, χ^2=5.35, df=1, P<0.05).

Mortality was significantly higher in trees less than 30 cm gbh than for trees ≥30 cm girth (χ^2 =6.92 and 8.37 in Plots 1 and 2 respectively, P<0.01 for both). Annual mortality for trees less than 30 cm gbh was 3.45% (Plot 1) and 3.28% (Plot 2), giving estimates of population half-lives of 20.1 years and 21.1 years respectively. For trees over 30 cm gbh mortality rates were 1.48% yr^{-1} in Plot 1, and 0.91% yr^{-1} in Plot 2, $t_{0.5}$ of 46.8 and 76.2 years respectively. In Plot 1, among trees ≥30 cm gbh in the major emergent species, mortality was greatest in *S. leprosula* and *P. malaanonan*, and lowest in *S. johorensis*, while no large trees of *S. pauciflora* died during this period. In

Table 6.1 Mortality rates (m, % yr, log model) of dipterocarp trees in Plots 1 and 2 between first enumeration (Plot 1: mid-September to mid-March 1986; Plot 2: mid-November to mid-December 1986) and July 1988. Size limits are gbh. Species are included under each plot heading only if their seedlings were present in the seedling study area of the same plot; totals are given for Light Red Merantis (LRM) in both plots, and Dark Red Merantis (DRM) in Plot 1 only.

	Plot 1					Plot 2				
	All trees ≥10 cm			<30 cm	≥30 cm	All trees ≥10 cm			<30 cm	≥30 cm
Species	N	dead	m	m	m	N	dead	m	m	m
S joho	111	6	2.15	3.42	0.76	86	9	6.84	9.80	2.04
S arge	34	4	4.81	7.37	2.68	46	4	5.67	8.32	0.00
S lepr	47	4	3.33	4.19	2.76	13	0	0.00	0.00	0.00
S parv	97	12	5.13	8.49	2.35	108	3	1.76	2.71	1.03
S fall	189	13	2.78	3.11	1.24	178	5	1.78	1.93	1.34
S pauc	87	3	1.33	2.26	0.00	-	-	-	-	-
P mala	71	2	1.13	0.00	2.72	79	1	0.79	1.50	0.00
H nerv	6	0	0.00	0.00	0.00	93	8	5.61	6.93	0.00
V sara	15	1	2.72	4.69	0.00	16	0	0.00	0.00	0.00
S pilo	-	-	-	-	-	109	2	1.15	1.03	2.11
V duli	7	0	0.00	0.00	0.00	-	-	-	-	-
S agam	8	0	0.00	0.00	0.00	-	-	-	-	-
LRM	178	20	4.57	7.20	2.47	167	7	2.67	3.30	0.79
DRM	276	16	2.31	2.89	0.58	-	-	-	-	-
Total †	702	48	2.75	3.45	1.48	970	37	2.42	3.28	0.91

† Includes all dipterocarp species present.

virtually all species, mortality was higher in small trees. The only exception was *P. malaanonan*, in which the two trees that died were >30 cm.

6.2 TREE GROWTH RATES

Median and maximum growth rates for each tree species are given in Table 6.2. Tree growth rates are expressed as Relative Girth Growth Rate, RGGR, and absolute Annual Girth Increment (AGI), analogous to RGR and AHI for seedlings, Chapter 4.

Highest median growth rates were in the Light Red Merantis: highest were in *S. parvifolia*, 1.9 % yr^{-1} and *S. argentifolia*, 1.7 % yr^{-1}. Three species had median girth increments exceeding 1 cm yr^{-1}: *S. parvifolia*, 1.9 cm yr^{-1}, *S. argentifolia*, 1.7 cm yr^{-1}, and *S. johorensis*, 1.2 cm yr^{-1}. Maximum increments in these species exceeded 6 cm yr^{-1}. Growth rates in the remaining LRM, *S. leprosula* were lower. Lowest growth rates were in the canopy species *H. nervosa* and *V. sarawakensis*, in *S. agamii* and in the two DRMs, *S, fallax* and *S. pauciflora*. Median growth rate in *P. malaanonan* was low, although the maximum rate was high, and more similar to the LRMs, at 5.85 cm yr^{-1}.

6.3 COMPARISON OF TREE & SEEDLING GROWTH & MORTALITY RATES

RGR values for Plot 1 trees cannot be compared directly with seedling RGRs because girth was the measure for trees, while height was used for seedlings. However, the rank of growth rates can be compared. Median growth rates, both relative and absolute, were not rank correlated ($P>0.05$). Much of the difference in rank between trees and seedlings is accounted for by *V. dulitensis*: the seedling population consisted of large numbers of very small seedlings, which had relatively low growth rates, whereas only five trees were present, each of which had positive increments, resulting in a high ranking compared to other species.

Maximum relative growth rates of trees and seedlings were significantly positively rank correlated ($r_s=0.647$, $P<0.05$, $n=11$), but absolute increments were not

Table 6.2 Median and maximum growth rates (Relative Girth Growth Rate, RGGR, % yr^{-1}, Annual Girth Increment, AGI, cm yr^{-1}) of dipterocarp trees (≥10 cm gbh) in Plot 1 (4 ha) for the period between mid-September 1985 to mid-March 1986 and July 1988. Species are included only if their seedlings were present in the 2 ha seedling study area of the plot. For maximum growth rates, initial girth (cm) of individual tree is given in brackets.

Species	Number of trees	Median		Maximum	
		RGGR	AGI	RGGR	AGI
S joho	79	2.20	1.23	32.5 (13.2)	6.54 (13.4)
S arge	21	2.70	1.69	23.2 (12.1)	6.41 (20.0)
S lepr	38	2.50	0.75	13.1 (23.6)	5.72 (65.2)
S parv	76	5.10	1.94	29.3 (15.5)	7.80 (68.0)
S fall	168	0.65	0.11	16.8 (19.8)	4.21 (19.8)
S pauc	73	0.60	0.13	12.4 (10.3)	4.42 (43.4)
P mala	63	1.00	0.33	9.5 (12.6)	5.85 (63.5)
H nerv	5	1.80	0.30	7.6 (12.5)	1.22 (15.1)
S agam	8	0.40	0.05	1.9 (11.8)	0.40 (108.0)
V duli	5	3.30	0.71	5.4 (12.3)	4.76 (91.8)
V sara	11	0.20	0.12	2.2 (26.5)	1.93 (87.3)

(r_s=0.503, P>0.05). Species which produced high relative growth rates as trees also produced the highest relative growth rates as seedlings, while species with low maximum growth rates as trees also had low maxima as seedlings.

Mortality rates were higher in seedlings than in trees in virtually all species. Exceptions were *V. sarawakensis* in Plot 1, in which the chance death of one out of 15 trees resulted in a relatively high mortality rate; no seedlings died. In Plot 2, tree mortality rates were higher than seedlings in *S. johorensis* and *H. nervosa*. In the seedling populations in these species, there was no clear trend in variation in mortality with size, and both species had a peak in mortality in seedlings over 2 m tall. In *S. fallax* in Plot 1, mortality rates were notably constant from seedlings ≤50 cm tall up to trees ≥10 cm gbh.

Tree and seedling mortality rates were not significantly rank correlated (r_s=0.514, n=11, P>0.05). The main differences in rank were in *S. parvifolia*, which had the highest mortality of trees, but was ranked fifth for seedling mortality, and both *S. johorensis* and *S. pauciflora* were ranked higher for mortality in seedlings than in trees. In general, however, as in seedlings, trees of the LRM group had the highest mortality rates, DRMs and *S. johorensis* were intermediate, and lowest rates were in the canopy trees. There was no significant rank correlation in Plot 2 (r_s=0.217, n=9, P>0.05).

Within trees, growth and mortality rates were not rank correlated across species (r_s=0.276, P>0.05).

6.3.1 Mortality and recruitment

Recruitment, defined as seedlings which grew into the 10 cm or greater girth class in the period between first enumeration of Plot 1 and July 1988, was compared with mortality of trees over the same period for different species within the two hectare seedling study area (Figure 6.1). In total, 37 trees died and 29 were recruited over the enumeration period (2.7 years), giving a mortality rate of 3.31% yr^{-1} and a recruitment rate of 2.40% yr^{-1}. If species not recorded as seedlings are excluded, (n=9, of which two died), the estimates become 2.53% yr^{-1} for mortality and 3.17% yr^{-1} for recruitment. In individual species, mortality was closely balanced by recruitment (Figure 6.1).

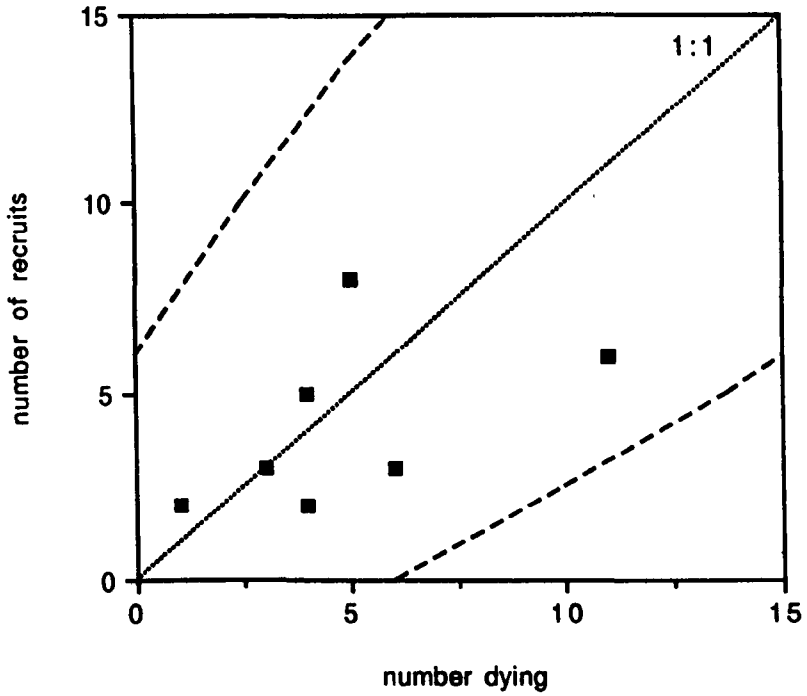


Figure 6.1 Comparison of the numbers of dipterocarp trees (≥10 cm dbh) dying, and numbers recruiting into the ≥10 cm gbh class in the seedling study area (2 ha) of Plot 1, during the period between August and December 1985 and July 1988 (recruits and/or dead trees were recorded in only seven species). Diagonal dotted line shows mortality equal to recruitment, and dashed lines give 5% confidence limits.

CHAPTER 7

SPATIAL PATTERNS OF SEEDLINGS AND TREES

7.1 INTRODUCTION

In forests, the patterns of trees and their seedlings are the outcomes of dynamic processes acting over many years. One of the major determinants of seedling dispersion pattern in the initial dispersal of propagules (Howe & Smallwood 1982). Subsequent growth and mortality then interact to alter the original pattern (Augspurger 1983a, 1984a,b, Augspurger & Kelly 1984, Becker & Wong 1985, Clark & Clark 1985, DeSteven & Putz 1984). Environmental heterogeneity will impose a pattern on species dispersions. In tropical forests, the creation of gaps, random and unpredictable in nature, is an important cause of spatial heterogeneity (Richards & Williamson 1975, Hartshorn 1978, Whitmore 1984, Brokaw 1985b, Armesto *et al.* 1986). Investigation of the types and scales of patterning found, and the variation between species may allow inferences to be made on some of the underlying processes controlling species diversity and forest dynamics.

Original observations of long distances between conspecific trees (eg. Alfred Russell Wallace [1878], Richards [1952]) have not been borne out by recent studies. Most tropical forest trees have been shown in fact to have clumped or random distributions (Greig-Smith 1952b, Poore 1968, Ashton 1969, Fox 1972, Hubbell 1979, Forman & Hahn 1980, Thorington *et al.* 1982, Hubbell & Foster 1983, Whitmore 1984, Armesto *et al.* 1986, Newbery *et al.* 1986, Ho *et al.* 1987). The large distances observed are merely a consequence of low density populations, and inter-tree distances are rarely further than expected (Lieberman & Lieberman, in press).

The spacing mechanisms of Janzen (1970) and Connell (1971), reviewed by Howe & Smallwood (1982) and Clark & Clark (1984), and the compensatory mechanisms proposed by Connell *et al.* (1984), have been postulated to explain spacing of trees. Evidence for the existence of these mechanisms can be inferred from comparison of seedling and tree dispersion patterns, and from differences in the distribution of different size classes (Clark & Clark 1984). Are larger individuals less clumped than smaller individuals? Are trees more spaced than their seedling patterns would predict? Caution must be exercised when extrapolating from the results of seedling studies to processes operating at the scale of adult trees - the spatial scales may be very different, and the same processes may not be relevant (Wiens 1989, Schupp 1992, Lieberman & Lieberman in press).

Many references to dipterocarp seedling pattern comment on the gregarious nature of the seedlings, clustered around reproductive adults (Poore 1968, Ashton 1969, 1982, Fox 1972, 1973, Liew & Wong 1973, Chan 1980, Whitmore 1984). Spatial patterns of dipterocarp seedlings have been recorded mainly by foresters concerned with quantifying the presence of regeneration in species important in timber production. The method commonly used was to lay out milliacre plots (approximately 2 m x 2 m) either randomly or along transects (Fox 1967, 1972, 1973; Liew & Wong 1973, Chan 1980). There is no information on larger scale patterns from fully-mapped seedling populations.

7.1.1 Aspects of pattern

Characteristics of pattern which can be described using different tests, and which could have explanations relevant to seedling dispersal patterns include: patch size (size of seedling shadow), distance between patches (distance between parents), and density of points within the patch (fecundity of parent tree, interacting with seedling competition). As well as the mean, the frequency distribution of these characteristics will yield more information, and could vary between species.

Perceived pattern is not independent of scale of observation. On the large scale, environmental heterogeneity is often the main factor influencing plant distribution. On a smaller scale, interactions between plants (competition, seed dispersal) are more likely to determine the observed patterns. A species may be distributed in a hierarchy of patch sizes, and characteristics of the pattern could be

described for each level (Hurlbert 1990). For example, a species may be confined to areas of suitable habitat, on a scale of hundreds of metres. Within this area individuals could be clumped around reproductive adults on a scale of tens of metres. Within these patches, enhanced survival in canopy gaps may impose further patchiness on a yet smaller scale, (less than 10 m).

The pattern may vary at different levels in the hierarchy. Trees could be regularly spaced within a patch, or patches may be randomly spaced. Detection of these possibilities is a function of scale. For example, a species may occur in large patches, covering several hectares, within which the distribution is random. Viewed in a two hectare plot the dispersal pattern of that species will appear to be random. If the study area happens to lie on the edge of the patch, the pattern would be described as aggregated on the scale of two hectares. Some tests give no information on the scale of aggregation, or repetition of clumping: a species detected as aggregated may be distributed in several patches, or a single patch within the study area.

7.1.2 Analysis of spatial pattern

Analysis of spatial patterns can be divided into several stages. The starting point is to test if the pattern differs significantly from random: rejection of randomness is a 'minimum pre-requisite' for further analysis (Diggle 1983), and should act only as a guide to the underlying biological processes (Greig-Smith 1983). Further tests are then used to explore the data and to suggest alternatives to randomness.

The chosen test or index should provide an indication of degree of departure from randomness, through the value of the test or the attained significance levels. Detection of degree of aggregation is always a function of scale. The test should give some insight into the scale of the pattern, and variation in the pattern with changing distance. Ideally, combinations of different tests should be used to show nature of departure from randomness (Diggle 1983). The analysis merely describes the pattern, or certain defined aspects of it. From this it may be possible to make inferences about the characteristics of the pattern, and the actual patches of plants - their size, spacing, or density (Hurlbert 1990). One could then go on to suggest biological mechanisms which could have produced the observed pattern.

This suggests a further desirable property of the chosen test: that it should have a simple biological interpretation (Hurlbert 1990), for example the actual distance between points, or the chance of two individuals occupying the same sub-area (quadrat). A further stage would be to attempt to model the underlying process of which the observed pattern is a realisation.

7.1.3 Alternatives to randomness

Testing against a null hypothesis of randomness is the starting point of any analysis of spatial pattern. The observed point pattern is usually tested for difference from the Poisson distribution, the simplest model of random arrangement of points. There is no interaction between points, and each point is an independent observation from a Poisson distribution (Ripley 1986).

A random pattern could still be produced by contradictory forces - by mechanisms which require explanation, despite the pattern showing no order (Dacey 1964, in Upton & Fingleton 1985). For example, limited seed dispersal, a clustering mechanism, may produce an initially aggregated pattern, but inhibition or thinning processes (competition for light or nutrients) acting later, may result in a distribution which is indistinguishable from random. Having rejected randomness, the two alternatives to consider are aggregated and uniform distributions.

7.1.3.1 Aggregated distributions

The patterns of seedlings clustered below a reproductive adult, or regeneration in a gap are obvious examples of aggregated distributions. Aggregated patterns are often found in tropical tree populations (eg. Richards & Williamson 1975, Forman & Hahn 1980, Armesto *et al.* 1986, Newbery *et al.* 1986). Scale is important in describing an aggregated pattern. Other characteristics such as patch size, patch density and inter-patch distance can also be described, depending on the choice of test. Two mechanisms can produce detectable aggregation: true contagion, and environmental heterogeneity (Diggle 1983). The two are often difficult to separate by tests of pattern. The distinctions are ones of scale and biology, and further information is usually needed before they can be made (Diggle 1983, Greig-Smith 1983). In practice, both are likely to be important mechanisms in producing the observed seedling spatial patterns (limited seed dispersal is a contagion mechanism, while gaps are an example

of environmental heterogeneity). A pattern that is heterogeneous, i.e., in which density varies over the sample area, can appear to be clustered if equal density (homogeneity) is assumed (Ripley 1981). The assumption of homogeneity is therefore an important condition of most tests.

Aggregated patterns can be modelled. A useful model for seedling distributions is the Poisson cluster process of Neyman and Scott (1972). Parent events are located at random, then a number of offspring per tree and their location relative to the parent are chosen, both independent observations from a specified distribution. The pattern defined by the model can be compared with the observed population.

7.1.3.2 Regular distributions

Regular, or inhibited, patterns have a more even point intensity than in a random arrangement, and lack small inter-point distances. The hardcore models (Ripley 1977), in which there is complete inhibition within a specified radius of each point, are too extreme for most biological situations where individuals can vary in size and shape (Cormack, in Upton & Fingleton 1979). The softcore models of Strauss (1975) are more realistic in defining biological interactions in which the probability of encountering a neighbour is a function of distance from each point.

An example of inhibition is in the spacing of large trees in the canopy. Crown volumes are not likely to overlap, leading to a degree of inhibition on the scale of 10 to 20 metres, but since crowns are plastic in size and shape, inhibition will not be complete. In Plot 1, for example, there were two large emergent dipterocarps (diameters 115.6 cm and 80.0 cm) located less than five metres apart.

7.1.3.3 Model fitting

An aim of some studies of tree pattern is to attempt to model the underlying process of the pattern, using clustered or regular alternatives to randomness (eg Ripley 1981, Diggle 1983, Franklin *et al.* 1985, Sterner *et al.* 1986). Large data sets, with N more than a few hundred, or data from a large spatial area, are often so heterogeneous that the assumptions of most models, those of isotropy, and particularly stationarity (Ripley 1981, 1986), can no longer be met (Diggle 1983).
One approach would be to split the plot into two halves, to formulate the model using data from one half, and test the model by fitting to the data from the remaining half. But, if the pattern is not stationary, it is not likely to be replicated in the two

halves, and the model will be invalid anyway. Another problem is that the two halves of the plot are not spatially distant, so are not strictly independent (Diggle 1983). In plot 1, for example, seedlings were distributed in single patches in two species, and in other species density differed between the two halves; these distributions were clearly not stationary. Fitting a model to an observed pattern does not provide an explanation for the pattern (Pielou 1977), but gives more information on the parameters of the pattern.

Therefore, the analyses carried out were exploratory in the sense that the aim was to describe the observed distribution patterns, and to attempt to make inferences on certain aspects of the patterns, specifically patch size and frequency. A further aim of many investigations of patterns is to 'formulate biological hypothesis which can then be investigated by non-statistical means' (Diggle 1983). In studies of forest dynamics, these hypothesis could include measurements of seed dispersal distances, seedling recruitment and survival, shade tolerance and response to gap creation as well as long term observations on species growth and survival rates from marked individuals.

7.1.4 Methods of analyses

There are two main methods for analysing spatial patterns. The first uses the variation in counts of individuals in quadrats, and the second uses the actual distances between points. Both types of method can be applied to fully-mapped patterns (Diggle 1983, Upton & Fingleton 1985).

7.1.4.1 Quadrat methods

Quadrat-based methods look at the variation in the number of points in sub-areas. If the pattern is random, the quadrat counts are observations from a Poisson distribution, and will have the variance equal to the mean. If the points are regularly distributed, the variance of the quadrat counts will be low relative to the mean, and if the points are aggregated, the variance will be higher than the mean, since some quadrats will contain patches of points. The ratio of variance to mean provides a basis for several indices (eg. Greig-Smith 1952a, David and Moore 1954, Lloyd 1967).

A problem with many of these indices is their dependence on the choice of

quadrat size, and therefore, once quadrat size has been chosen, information on the pattern is relevant only to that scale. Secondly, interpretation of the results can be difficult (Ripley 1978) and significance testing problematic (Diggle 1985, Hurlbert 1990). Thirdly, in a fully-mapped population, the position of points within the quadrats, and the relative positions of the quadrats themselves, are not used. Finally, while all Poisson patterns will have a variance:mean ratio of 1, not all patterns with a variance:mean ratio of 1 are Poisson patterns (Pielou 1977), and can be distinctly non-Poisson (Hurlbert 1990).

Contiguous quadrat counts are useful for large and potentially heterogeneous data-sets (Diggle 1983). Because of problems with significance testing, their use is best confined to exploratory analysis (Greig-Smith 1979). Unlike distance-based methods, quadrat methods are not influenced by edge effects.

7.1.4.2 Distance based methods

A variety of tests exist based on actual distance between points in a fully mapped pattern. These can be plant-to-plant or point-to-plant distances (Upton & Fingleton 1985). Within plant-to-plant distances, there is the choice of looking at distance from each plant to its nearest neighbour (NN), or at all inter-plant distances.

Use of NN distances focuses on the small scale, at the distances over which plants interact directly, for example in competition for light, nutrients or water. Using all inter-plant distances explores the patterns over larger distances, for example at the scale of whole seedling shadows, or distances between patches. Both approaches give useful insights into the observed patterns, and are relevant to different aspects of the plant's biology.

7.2 METHODS

The approach to analysing the seedling spatial patterns was to use a variety of tests to investigate the data. Each test explored a different aspect of the pattern. Initially, a simple index (the Clark-Evans test) was used to test for departure from randomness in each species population. Further tests were chosen to explore and describe the patterns in more detail, and at a range of spatial scales.

Comparison of the distribution patterns of different species was the main aim.

The degree of departure from randomness as measured by the significance levels attained in each test was used to compare species. Combinations of different tests may reveal the nature of departure from randomness and provide more insight into variation in pattern with scale. Combined with the results from Chapter 8 on the relative dispersion of adults and seedlings, the aim was to give a fuller picture of the nature of, and differences between, the spatial patterns of seedlings in different species. A further aim was to compare results from the different tests to see if interpretations of the patterns in each species were consistent.

Four tests were chosen, two distance based tests: the Clark-Evans test (Clark & Evans 1954), and refined NN analysis (Diggle 1979, 1983); a quadrat-based method, Morisita's Index (Morisita 1959), and a combined count and distance measure, second-order analysis using Ripley's K(t) function (Ripley 1976). There follows a description of each test in terms of its desirable features and disadvantages, together with the rationale for its use. The methods of calculation of each test are described in detail.

7.2.1 The Clark-Evans test

The Clark-Evans test (Clark & Evans 1954) was chosen to provide a quick initial test of departure from randomness. The test result is a single value, which gives no information on the scale of pattern, nor on any variation with distance. It incorporates a test of significance so that magnitude of departure from randomness can be assessed. It is easily interpretable in biological terms: a mean NN distance of say 1.7 m can be compared to an expected of 2.8 m, and envisaged in the field. But, since only NN distances are used, and only their mean, much information is not used, especially in a fully-mapped population.

The test compares the observed mean nearest-neighbour distance, w, with the expected mean, E(W), in a random distribution, calculated from point density:

$$E(W)=0.5\sqrt{(A/N)}$$

where N is the number of individuals in the area A, and A/N is the estimate of density. The ratio of w to E(W), R, is the proposed measure of the departure of the observed distribution from random expectation. In a completely random distribution R=1 [since w = E(W)]. Values of R less than 1 indicate aggregation (the observed NN distances are shorter than expected), R=0 being the maximum aggregation (all individuals at the same point and therefore w = 0). Values of R greater than 1

indicate a degree of regularity.

Clark & Evans (1954) proposed a significance test for departure from randomness:

$$CE = \{w - E(W)\} / var(W)$$

referring CE to the normal distribution. There are two problems when NN distance is measured from all possible points. First, the normal distribution of CE assumes that all NN distances are independent. Secondly, edge effects means that points near the boundary will tend to have larger NN distances than points nearer the centre of the area. Thus E(*W*) will be underestimated and the test biased towards regularity. In fact dependence among NN distances has little practical effect on the test (Diggle 1983), but edge effects can make a significant difference. Sinclair (1985) has shown that use of the uncorrected test can lead to spurious claims of significant departure from randomness, especially for areas with elongated boundaries. One way of overcoming the problem of edge effects is to use a border zone, allowing points in an outer zone to be nearest neighbours but not focal points (Clark and Evans 1954). Apart from the difficulty of choosing the width of the buffer zone, this results in the non-arbitrary loss of points. Donnelly (1978) suggested corrections to the variance and expectation to adjust for edge effects. The correction factors were derived by a combination of simulation and integration, and take into account the perimeter, P, of the study area,

$$E(W) = 0.5 \sqrt{(A/N)} + 0.0514P/N + 0.041\ P/N^{3/2}$$

and

$$var(W) = 0.0703A/N^2 + 0.037P \sqrt{(A/N^5)}$$

The corrected version of the Clark-Evans test was found by Ripley (1979b) to be powerful at detecting both regular and aggregated distributions. The corrected version of the test was therefore used to test seedling pattern, in preference to the use of a buffer zone.

7.2.2 Morisita's Index

Morisita's Index of Dispersion is a simple quadrat-based measure of departure of spatial dispersion from Poisson expectations (Morisita 1959). It was derived from Simpson's (1949) diversity index, and can be expressed as the ratio of the observed probability of picking two conspecific individuals at random from a quadrat to the

expected probability if the individuals are randomly distributed over all quadrats (Hubbell 1979). Thus, an index value of 1.5 has the interpretation that the points are 50% more crowded than if they were randomly dispersed.

If N points are distributed over a sample area divided into q contiguous, equal-sized quadrats, and n_i, i=1...q is the number of points in the ith quadrat, then:

$$N = \Sigma n_i$$

and

$$\delta = \Sigma\, n(n-1) \,/\, N(N-1)$$

is an unbiased estimate of Simpson's measure of population diversity, Σp_i^2 , where p ...p_i is the proportional abundance of the ith out of S species. Morisita's Index is found by multiplying by q, the number of quadrats:

$$I_m = q\delta$$

The Index will equal 1.0 if the points are distributed at random (because $\delta = 1/q$ if the distribution of points in quadrats is Poisson). If the points are uniformly distributed, I_m will be less than 1.0, and if points are aggregated I_m will exceed 1.0. In the most extreme case where all points are in one quadrat, δ will equal 1 and therefore $I_m = q$.

Morisita (1959) proposed testing the significance of I_m by referring to the F distribution:

$$F^{n1}{}_{n2} = I_m(N-1)+q-N \,/\, q-1$$

where $n_1 = q-1$ and $n_2 = \infty$. The numerator is the "Index of Dispersion" based on the variance/mean ratio (David & Moore 1954), which has a χ^2 distribution and can be referred directly to χ^2 tables (Greig-Smith 1983). Because I_m has a χ^2 distribution, the same requirement applies of a minimum expected value of 5 per cell (quadrat) (Diggle 1983) although Sakai & Oden (1983) suggest that this limit may be necessary only where point distribution is regular, and for clumped populations a lower limit of a mean of 3/5 points per quadrat may be sufficient. Quadrat-based indices are generally robust methods of testing spatial patterns (Diggle 1983). An important feature of I_m is that it is independent of population density (Pielou 1969, Hill 1973).

The index is calculated for a range of quadrat sizes. Variation in the curve of Im plotted against quadrat size give information on the dispersion of points within patches, and on the distribution of the patches. Different configurations of within and between patch dispersion patterns, and associated I_m values, are illustrated by Morisita (1959) and Hubbell (1980).

Morisita's Index has been extensively used in studies of plant spacing (eg. Richards & Williamson 1975, Williamson 1975, Hubbell 1980, Sakai and Oden 1983, Howe and Wright 1986, Platt *et al.* 1988, Read & Hill 1988). Recently, the Index has fared well in a study of the unique dispersion patterns of the montane unicorn (Hurlbert 1990). In the present study, significance testing was not carried out on Morisita Index values because of reservations over the use of χ^2 tests with contiguous (i.e. non-independent) quadrats (Hurlbert 1990).

7.2.3 Refined nearest neighbour analysis, G(*w*)

More insight is gained from looking at the complete distribution of NN distances, rather than just the mean, in what has been termed refined NN analysis (Diggle 1979, 1983). The theoretical distribution function, G(*w*), of NN distances in a random pattern is known, and depends on the number of points, n, in the area A, where for large n, density λ=A/n:

$$G(w) = 1-\exp(-\lambda\pi w^2)$$

but this ignores edge effects (Diggle 1983). To adjust for edge effects, the estimate of $\hat{G}(w)$ for the observed NN distance distribution can be weighted by excluding those points which are nearer to the plot boundary than to their nearest neighbour within the plot (Upton & Fingleton 1985). However, this involves discarding a non-random, and potentially large portion of the data. A better approach is to generate a series of random data sets, and compare the observed distribution of NN distances, $\hat{G}(w)$, with the mean, $\dot{G}(w)$, and significance envelope derived from the simulations. Edge effects will be the same for both the simulated and observed data sets (Diggle 1983). If $\hat{G}(w)$ lies outside the envelope, this indicates significant departure from randomness at the scale of the corresponding w values; if $\hat{G}(w)$ is above the envelope, significant aggregation is indicated, if below, regularity. The maximum and minimum of the values of G(*w*) from 99 simulated random data sets for each species were used to generate 1% confidence limits.

A test statistic for assessing overall magnitude of departure from randomness was d_w, defined as the maximum difference, over the range of w, between the mean, $\dot{G}(w)$, of the simulations and the observed value, $\hat{G}(w)$, (based on a suggestion in Diggle 1983). To assess significance of overall departure from randomness, d_w from the observed distribution was compared with the values of d_w obtained from each of

the 99 simulations for each species. The values of d_w allow comparison between species of the degree of departure from randomness.

Refined nearest neighbour analysis has been used by Kenkel (1988) to assess spatial pattern of Jack pine trees.

7.2.4 Second-order analysis, Ripley's K(*t*)

The combined count and distance measure, K(*t*), of Ripley (1976, 1977, 1978) provides a means of describing pattern at a range of scales. Since all inter-plant distances are used, the pattern is described at a wider range of scales than by using only NN distances.

The function K(*t*) characterises the second-order properties of a point pattern, the variation in distances between points. (The first-order property is intensity, in the same way that mean and variance are the first and second order properties of a one-dimensional set of numbers). When multiplied by intensity, λ, it has the definition (Ripley 1976):

$\lambda K(t)$ = the expected number of further points within distance t of an arbitrary point.

An advantage of K(*t*) is that the theoretical function is known for the Poisson distribution. The area within distance t of a point is πt^2, and the expected number of points within that area is $\lambda \pi t^2$. Therefore, for a Poisson forest:

$$K(t) = \pi t^2$$

A useful variant is

$$L(t) = \sqrt{\{K(t)/\pi\}}$$

In a Poisson forest,

$$t - \sqrt{\{K(t)/\pi\}} = 0 \quad \text{and} \quad L(t) = t$$

The square root transformation, suggested by Besag (1977), stabilises the variance over the range of t. Also, by linearising the plot of L(*t*) against t, the small distance end of the plot is clearer.

To estimate $\hat{K}(t)$ from data, the effect of the edge must be taken into account. Ripley's (1976) method, for N points in an area A, is

$$\hat{K}(t) = A \sum\sum k(x,y) \; / \; N$$

where the sum is over all pairs of points at distance t or less apart. The function

k(x,y) is a weighting factor to adjust for the probability of encountering x, since some individuals at distance t from point x may be outside the study area. The function is defined as the inverse of the proportion of the circumference of the circle centred on x and passing through y which is within the study area. The double summation includes k(x,y) and k(y,x), which are not necessarily the same. As t increases, the weighting function can become unbounded, and the sampling fluctuations increase (Diggle 1983), and therefore Ripley (1976) suggests an upper limit for t of $\sqrt{(A/2)}$.

Monte-Carlo simulation is often the best way to test patterns for departure from randomness (eg Upton & Fingleton 1985), but for $\hat{L}(t)$, Ripley (1976) suggested that 1% and 5% significance limits could be calculated from $1.68\sqrt{(A/N)}$ and $1.42\sqrt{(A/N)}$ respectively, and these were used in this study.

Ripley (1979, 1986) found that $\hat{K}(t)$ was among the most powerful of tests at detecting clustered distributions. $\hat{K}(t)$ and the variant $\hat{L}(t)$ have been used in several studies of pattern in forest trees and seedlings (Sterner *et al.* 1986, Getis & Franklin 1987, Kenkel 1988, Szwagrzyk 1990, Duncan 1991). A further advantage of $\hat{K}(t)$ is that the theoretical form of the function is known for certain other classes of point process, apart from simple Poisson processes, including Poisson cluster processes (Diggle 1979). The function is given by Diggle (1983) for a Poisson cluster process where the number of offspring per parent is Poisson and the dispersion of seedlings relative to adults follows a radially symmetric normal distribution. This seemed a reasonable starting assumption for dipterocarp trees and their seedlings. Similar models have been fitted to redwood seedlings (Diggle 1983) and pine trees (Ripley 1981). Plots of $\hat{K}(t)-\pi t^2$ versus t can be used to suggest initial estimates for the parameters of the model (Diggle 1983).

For a Poisson cluster process:

$$K(t) = \pi t^2 + \varrho^{-1} [1-\exp(-t^2 / 4\sigma^2)]$$

where ϱ is the mean number of parents per unit area, and $2\sigma^2$ is the mean squared distance from seedlings to adults (Diggle 1983). The maximum point on the plot of $\hat{K}(t)-\pi t^2$ against t equates to $(4\sigma, 1/\varrho)$, giving an estimate of number of parents and mean distance to parent. In this study, I compared the parameter estimates from the $\hat{K}(t)$ plots with the observed values. The reasons for not going on to construct and refine a model of the underlying processes were given earlier (Section 7.1.3.3).

To summarise, there were three aspects to the second-order analysis, $\hat{K}(t)$:

1) A formal assessment was made of overall departure from randomness in each species using L_{max}, the maximum difference between $\hat{L}(t)$ and t.

2) The range of distances over which $\hat{L}(t)$ differed significantly from random was examined by plotting $\hat{L}(t)$ against t and the calculated significance limits.

3) The plot of $\hat{K}(t)-\pi t^2$ against t was used to estimate the parameters of a Poisson cluster process. The estimates of number of adults and mean seedling-to-adult distance were compared with the observed values, and used to estimate seedling patch size.

7.2.5 Programme testing

Programmes to calculate the Clark Evans test, Morisita's Index, $\hat{G}(w)$ and $\hat{K}(t)$ were written in FORTRAN. The $\hat{K}(t)$ programme included subroutines provided by P. Diggle. Before analysing the seedling data, the programmes were tested in a number of ways. The programmes were run on simulated random data sets with x- and y-coordinates and number of points in the same range as the observed seedling data. 100 data sets were used to test the Clark-Evans and Morisita programmes, and ten for the $\hat{K}(t)$ programme. None of the programmes detected significant departure from randomness. All the programmes were run on three sets of regular data with points generated within a 100 m by 200 m area, at spacings of 5 m (number of points=861), 10 m (n=231) and 20 m (n=66). Each programme correctly detected regularity in the data sets. The programmes to calculate the Clark-Evans test, $\hat{G}(w)$ and $\hat{K}(t)$ were run on three data-sets given in Diggle (1983). The three sets (Japanese black pine saplings, redwood seedlings and biological cells) are examples of random, aggregated and regular patterns respectively. The results obtained were very similar to those found by Diggle (1983).

7.3 RESULTS

7.3.1 Clark-Evans test

The results of the Clark-Evans test are given in Table 7.1. In Plot 1, the test indicated significant aggregation in all species except *V. sarawakensis*. In Plot 2, all species were significantly aggregated except *S. leprosula* (the small sample size resulted in a large variance term which decreased the value of CE, despite the relatively low value of R).

The two *Vatica* species in Plot 1 lay at the extreme ends of the range of degree of aggregation. In *V. dulitensis*, the most strongly aggregated species, the mean NN distance was 0.3 m compared to the expected value of 2.5 m, while in *V. sarawakensis*, the least aggregated, the observed NN distance was 7.0 m and the expectation, 7.5 m.

The Clark-Evans test was calculated for each species in the two halves of Plot 1 separately. The results from the two halves were broadly similar. In both halves the dispersion of *V. sarawakensis* was indistinguishable from random. All other species were significantly aggregated in both halves of the plot. If species are ordered by the value of the ratio of observed to expected NN distance, R, species in the two halves were significantly rank correlated (Spearman r_s=0.836, n=11, p<0.01), indicating that patterns of species are similar in the two halves.

There was no relationship between the degree of aggregation and population size in either plot (Figure 7.1). While the most highly aggregated species, *V. dulitensis*, had the largest population size, and the least aggregated the smallest (*V. sarawakensis*), in between there were highly aggregated species with a relatively small population size (*H. nervosa*) and species with large N and low degree of aggregation (*P. malaanonan*).

7.3.2 Morisita's Index

The values of I_m plotted against the log of quadrat area for individual species are shown in Figure 7.2. All species show a similar pattern of exponential decline in I_m value with increasing quadrat size. This pattern is characteristic of a clumped population distribution, with density decreasing exponentially away from point

Table 7.1 Results of the Clark-Evans test. E(W) and w are the expected and observed mean nearest-neighbour distances, var(W), the variance and R, the ratio w/E(W). Absolute values of the test statistic CE, the standard normal deviate, exceeding 1.645 indicate significant departure from randomness at the 5% level (*); CE >2.33, the 1% level (**), and CE > 3.11, the 0.1% level (***).

(a) Plot 1

Species	N	w	E (W)	var (W)	R	CE	
S joho	333	3.05	3.97	0.0142	0.77	-7.68	***
S arge	245	3.24	4.65	0.0268	0.70	-8.61	***
S lepr	157	4.08	5.85	0.0672	0.70	-6.83	***
S parv	209	4.06	5.05	0.0372	0.80	-5.12	***
S fall	623	1.68	2.88	0.0039	0.58	-19.21	***
S pauc	554	2.13	3.06	0.0050	0.70	-13.16	***
P mala	587	2.33	2.97	0.0045	0.78	-9.56	***
H nerv	138	2.39	6.26	0.0879	0.38	-13.04	***
S agam	161	4.88	5.77	0.0638	0.84	-3.56	***
V duli	846	0.29	2.47	0.0021	0.12	-47.45	***
V sara	97	6.97	7.52	0.1833	0.93	-1.30	N.S.

(b) Plot 2

Species	N	w	E (W)	var (W)	R	CE	P
S joho	134	2.48	3.11	0.0222	0.80	-4.20	***
S arge	43	4.34	5.66	0.2417	0.78	-2.48	**
S lepr	18	7.48	9.11	1.5636	0.82	-1.31	N.S.
S parv	111	2.44	3.43	0.0329	0.71	-5.42	***
S fall	106	2.26	3.51	0.0362	0.64	-6.57	***
P mala	278	1.91	2.13	0.0049	0.90	-3.17	***
H nerv	275	1.53	2.14	0.0050	0.71	-8.61	***
S pilo	24	4.76	7.77	0.8402	0.61	-3.28	***
V sara	82	3.19	4.01	0.0620	0.79	-3.31	***

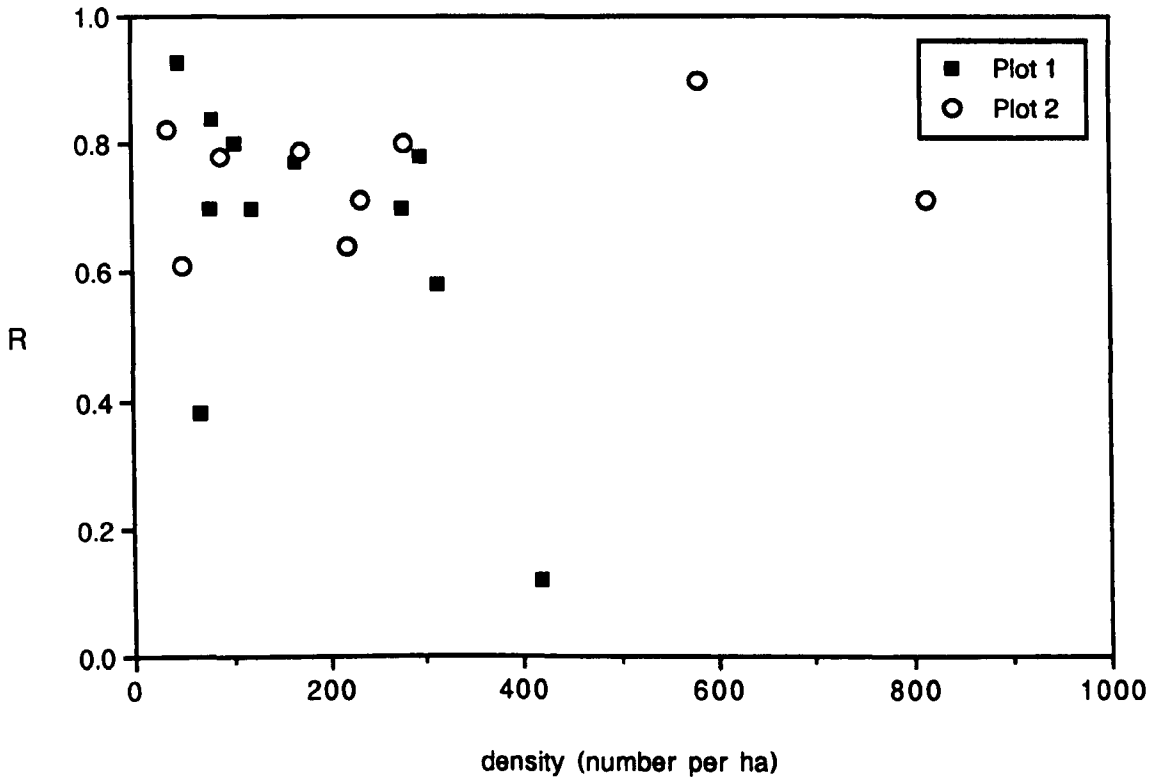


Figure 7.1
Relationship between seedling density (ha^{-1}) and R, the ratio of observed to expected mean nearest neighbour distance in different species in Plots 1 and 2.

sources of high density (Hubbell 1980), and suggests a pattern of seedling shadows around reproductive adult trees. For most species, maximum index values were in the smallest quadrat size, 2.5 m, indicating that maximal clumping occurred at the smallest scale tested, or smaller.

The values of I_m reached in the smallest quadrat sizes, and the rate of index decrease vary between species. In plot 1, *H. nervosa* had the highest value, which decreased rapidly with increasing quadrat size. Most *H. nervosa* seedlings were in a single clump at the northern end of the study area. In contrast, I_m values were relatively low throughout the range of quadrat sizes in *P. malaanonan* and *S. parvifolia*. These species were relatively well-dispersed throughout the study area.

I_m values for species in Plot 2 were very similar to those of the same species in plot 1, both in rate of change with quadrat size and in actual value (Figure 7.2(b)). For example, in both *P. malaanonan* and *S. parvifolia*, I_m was low and decreased slowly with increasing quadrat size in both plots, indicating that these species were well-dispersed in both plots. I_m values in *S. argentifolia* decreased rapidly with increasing quadrat size in both plots, suggesting that both contain multiple clumps of *S. argentifolia* seedlings with relatively high density at the clump centres (Morisita 1959, Hubbell 1980).

Variation between species groups

Plots of I_m for all species pooled (excluding *V. dulitensis*), and for the two major *Shorea* groups, Light and Dark Red Merantis, are shown in Figure 7.3. Curves for the two *Shorea* groups are very similar, showing a parallel exponential decline in I_m with increasing quadrat size. I_m values for Dark Red Merantis were slightly higher. I_m values for all species pooled showed a similar trend to that of the *Shorea* groups, but with lower index values than either group. Dipterocarp seedlings in total were better-dispersed throughout the plot than either group considered separately. This suggests that the two major groups are distributed in non-overlapping patches. If both groups occurred within the same space, the total population would be more clumped than either group.

Variation in pattern with size

I_m values are plotted for two height classes of seedlings, small (≤100 cm tall) and large (>250 cm tall) for species in Plot 1 in Figure 7.2(a). Large saplings were more clumped than small in five of the eight species: the three Light Red Merantis,

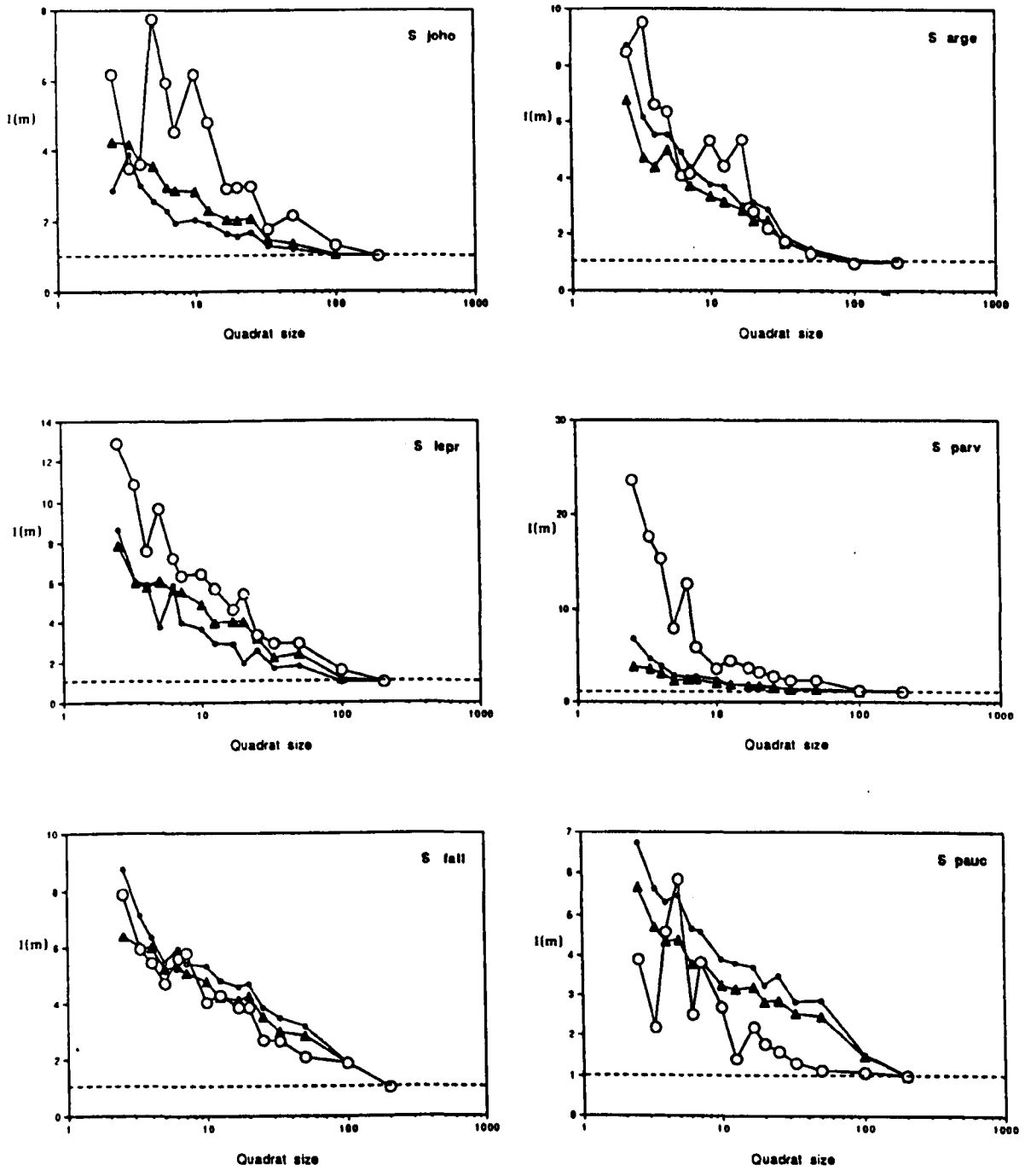


Figure 7.2 Values of Morisita's Index, I_m in a range of quadrat sizes (side length, m) in different species. The dashed line at I_m=1.0 is the Index value for a random distribution. ▲: all sizes; ◯: seedlings >250 cm; O: seedlings ≤100 cm.
(a) Plot 1

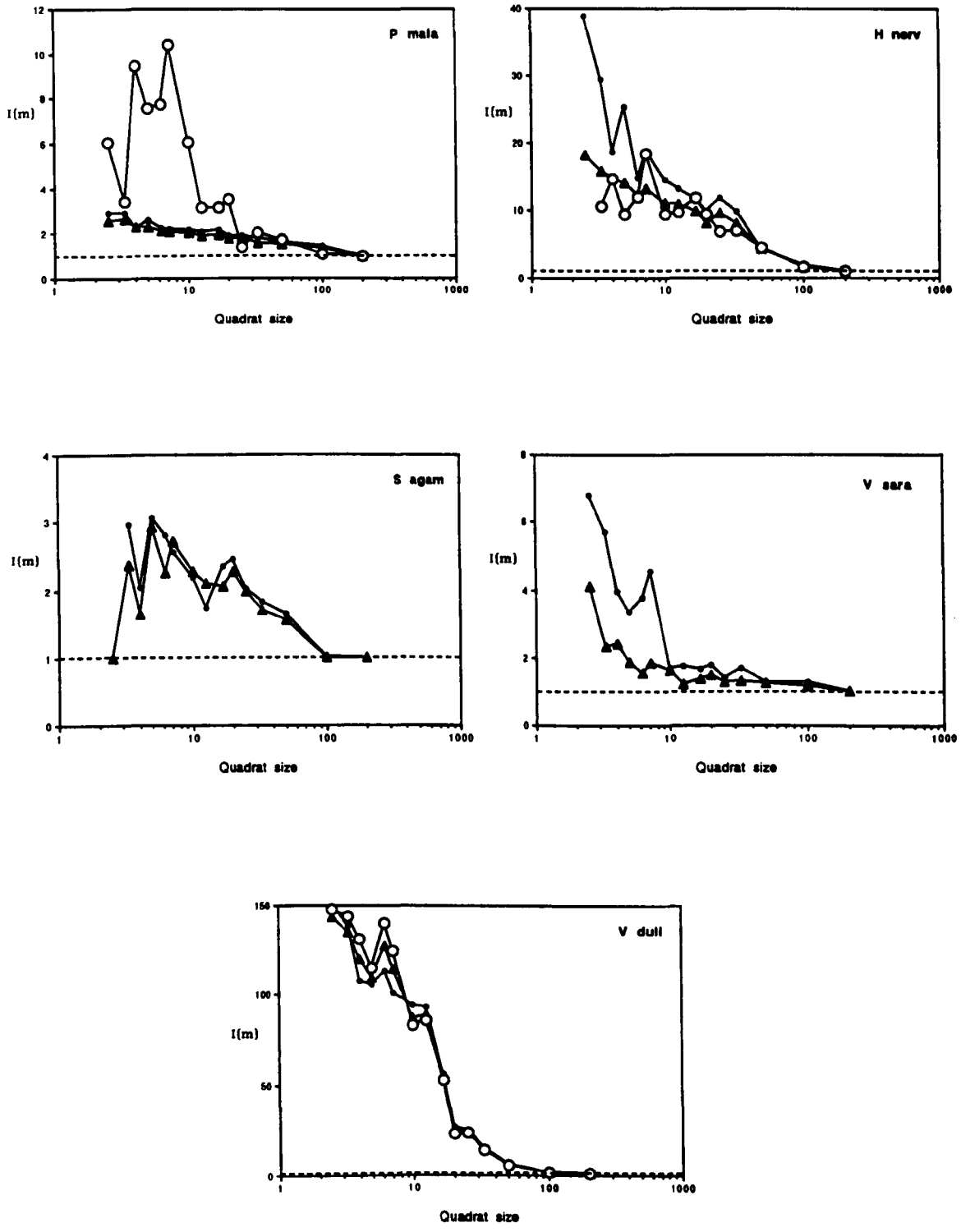
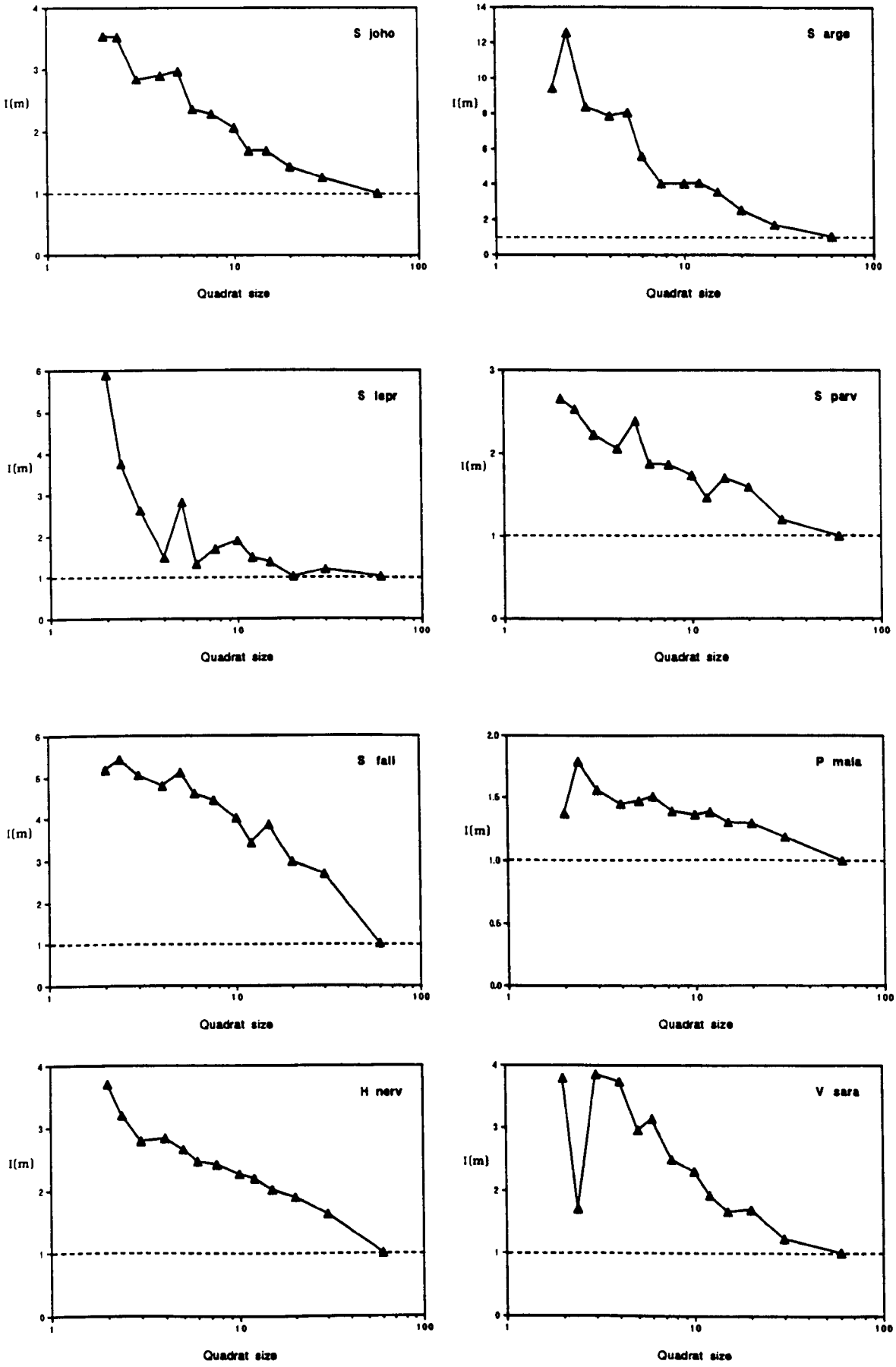


Figure 7.2 (continued) Values of Morisita's Index, I_m in a range of quadrat sizes (side length, m) in different species. The dashed line at I_m=1.0 is the Index value for a random distribution. ▲: all sizes; ◯: seedlings >250 cm; O: seedlings ≤100 cm.

(a) Plot 1

For *Vatica dulitensis*, symbols used are ▲: all sizes; ◯: seedlings older than 1985 cohort; O: seedlings of 1985 cohort.



(b) Plot 2 (all seedlings in each species)

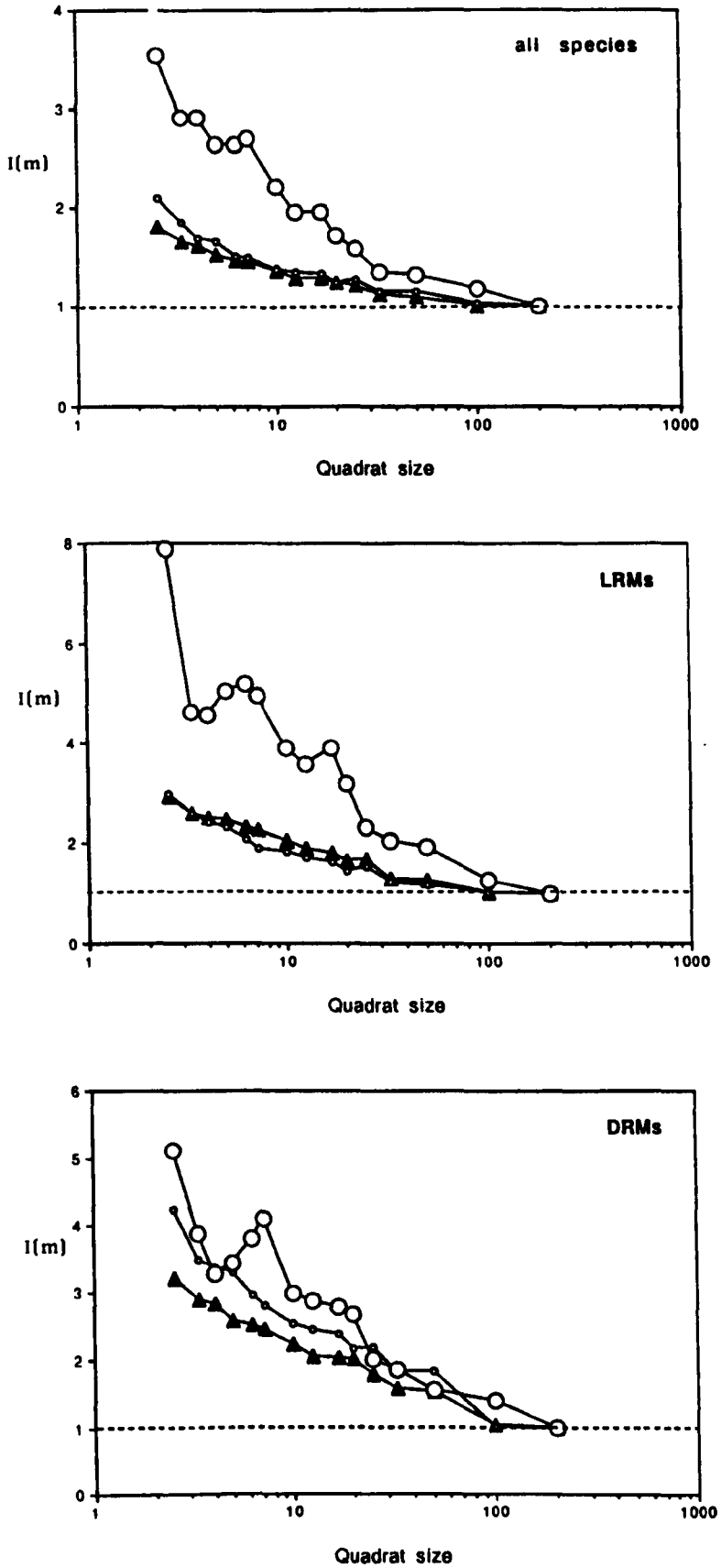


Figure 7.3 Values of Morisita's Index, I_m in a range of quadrat sizes (length of side, m) for all dipterocarp seedlings pooled (excluding *Vatica dulitensis*), and for Light Red Merantis (LRMs) and Dark Red Merantis (DRMs) in Plot 1. ▲: all sizes; ◯: seedlings >250 cm; O: seedlings ≤100 cm

S. johorensis and *P. malaanonan*. In *S. pauciflora*, small seedlings were more clumped than large seedlings, while in *S. fallax*, the two size classes have a similar degree of clumping. In *H. nervosa*, small seedlings were more clumped than large. The I_m curves of large saplings were notably irregular in the LRMs, with multiple peaks, not present in plots for small seedlings.

I_m values of large and small seedlings in the two Meranti groups are shown in Figure 7.3. In both groups, large seedlings were more clumped that small seedlings, but the difference was greater in the Light Merantis.

7.3.3 Refined nearest neighbour analysis, G(*w*)

The distribution functions of NN distances are shown in Figure 7.4 for each seedling population. The first graph of each pair shows $\hat{G}(w)$, the observed cumulative NN distance distribution, together with the mean, $\bar{G}(w)$, and maximum and minimum G(*w*) from 99 random simulations, plotted against $\hat{G}(w)$. The second graph in each pair shows $\hat{G}(w)$-$\bar{G}(w)$, clarifying the range of distances at which $\hat{G}(w)$ differed from $\bar{G}(w)$. The third aspect of this analysis of NN distances was formal significance testing, by comparing d_w for the seedling data [the maximum value of $\hat{G}(w)$-$\bar{G}(w)$] with the d_ws from each of the simulations (Table 7.2).

In ten of the 11 species, the observed d_w exceeded all the d_ws from the 99 simulations, leading to rejection of randomness in these species at the 1% level. In the remaining species, *V. sarawakensis*, the observed d_w was exceeded 12 times out of 99 random simulations, so that a random distribution cannot be rejected. The small sample size (N=97) resulted in broad significance limits (Figure 7.4), but d_w was still the lowest of any species (Table 7.2). If the magnitude of d_w is taken to indicate magnitude of departure from randomness, the greatest departure was in *V. dulitensis* and the least (of species with significant aggregation) was in *S. parvifolia*.

In all species except *V. sarawakensis* (Figure 7.4) the function $\hat{G}(w)$ lay above the upper limit of the simulation envelope, indicating that there was an excess of small NN distances, i.e. significant aggregation. The range of distances over which $\hat{G}(w)$ exceeded the upper limit varied between species (Table 7.2). The second graph of each pair illustrates the range of distances over which $\hat{G}(w)$ differed significantly from $\bar{G}(w)$ (Figure 7.4). In the most extremely aggregated species, *V. dulitensis*, the graph of $\hat{G}(w)$-$\bar{G}(w)$ peaked at 0.5 m, and examination of the plot of $\hat{G}(w)$ against $\bar{G}(w)$

Table 7.2 Results of refined nearest neighbour analysis, $\hat{G}(w)$. Maximum value of d_w, the difference between $\hat{G}(w)$ and $\bar{G}(w)$ and corresponding value of w are given for each species. Last column gives the distance over which $\hat{G}(w)$ departed significantly from random as assessed by simulation. (Values in brackets indicate that no significant departure from randomness was detected).

Species	Max d_w	Value of w (metres) at max d_w	Departure from random*	Distance range (metres)
S joho	0.286	2	agg reg	1.0 - 6.0 9.5 - 19.5
S arge	0.338	3.5	agg	0.5 - 6.5
S lepr	0.349	3	agg reg	1.0 - 9.0 14.5 - 23.0
S parv	0.176	3	agg	1.0 - 7.0
S fall	0.445	2	agg reg	0.5 - 5.5 8.5 - 25.0
S pauc	0.362	2	agg reg	0.5 - 5.0 7.0 - 21.0
P mala	0.233	2	agg reg	0.5 - 5.0 8.0 - 10.0 ; 11.0 - 25.0
H nerv	0.621	3	agg	0.5 - 11.0
S agam	0.216	4.5	agg reg	2.0 - 8.0 16.5 - 17.0
V duli	0.883	0.5	agg	0.5 - 6.0
V sara	(0.142)	(4.5)	N.S.	(1.0)

* agg: aggregated distribution
reg: regular distribution

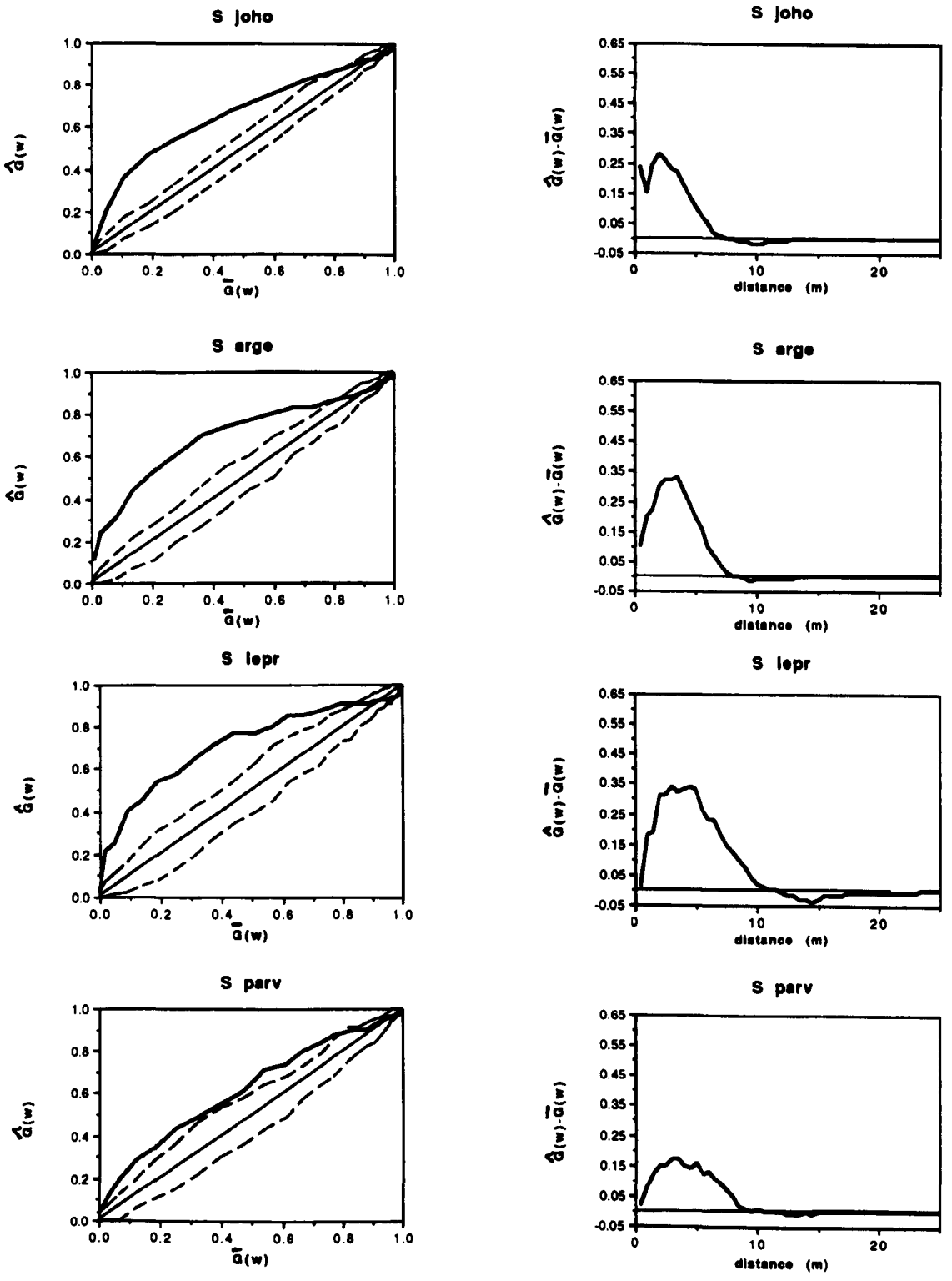


Figure 7.4 Results of refined nearest-neighbour analysis, G(w), of different species in Plot 1. The first graph of each pair shows the cumulative observed NN distribution $\hat{G}(w)$ (bold line), with mean, $\bar{G}(w)$, and maximum and minimum (dashed lines) G(w) values obtained from 99 random simulations in each species. The second graph of each pair shows $\hat{G}(w)$-$\bar{G}(w)$ plotted against distance (m).

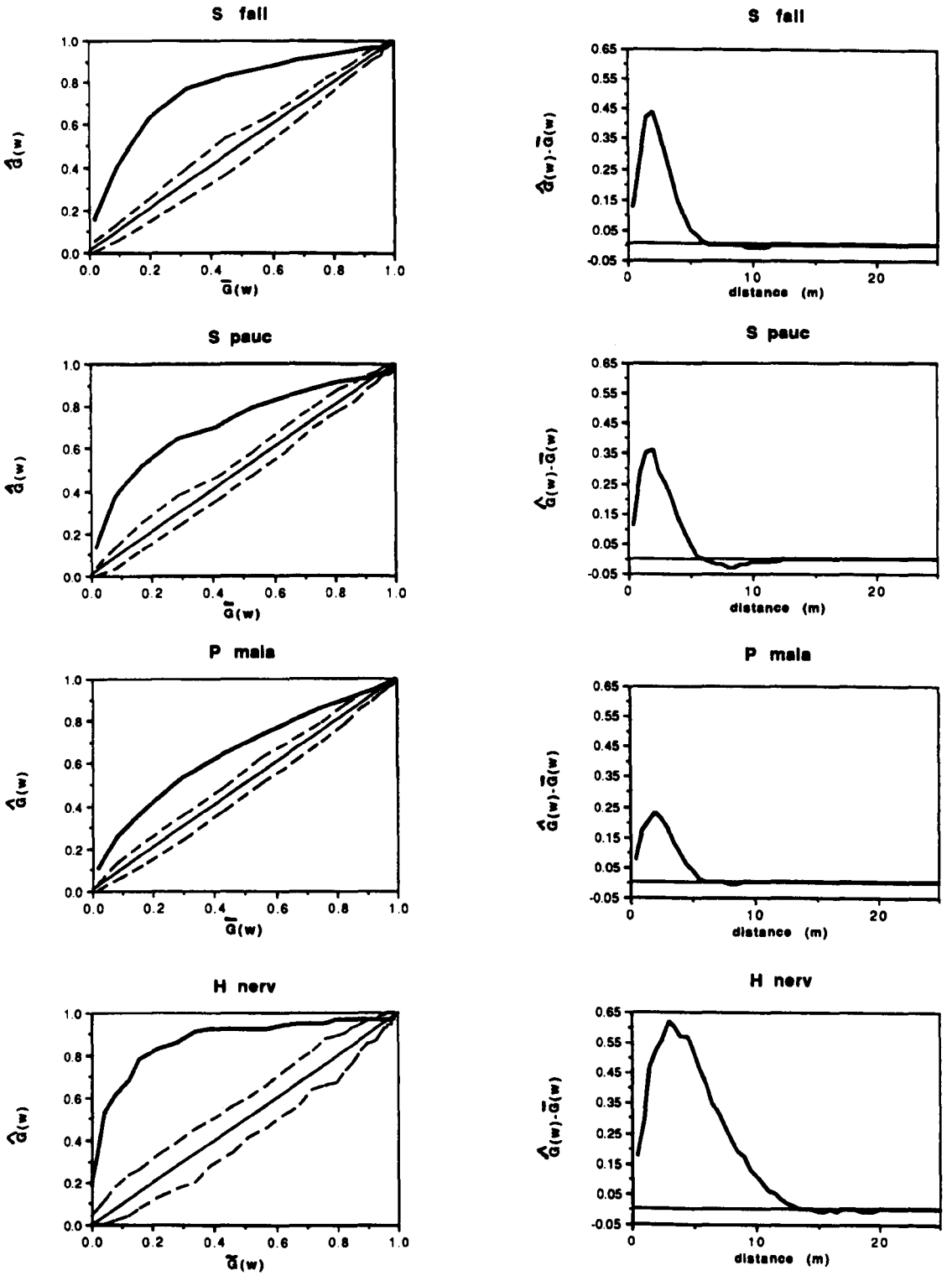


Figure 7.4 (continued) Results of refined nearest-neighbour analysis, G(w), of different species in Plot 1. The first graph of each pair shows the cumulative observed NN distribution $\hat{G}(w)$ (bold line), with mean, $\bar{G}(w)$, and maximum and minimum (dashed lines) G(w) values obtained from 99 random simulations in each species. The second graph of each pair shows $\hat{G}(w)$-$\bar{G}(w)$ plotted against distance (m).

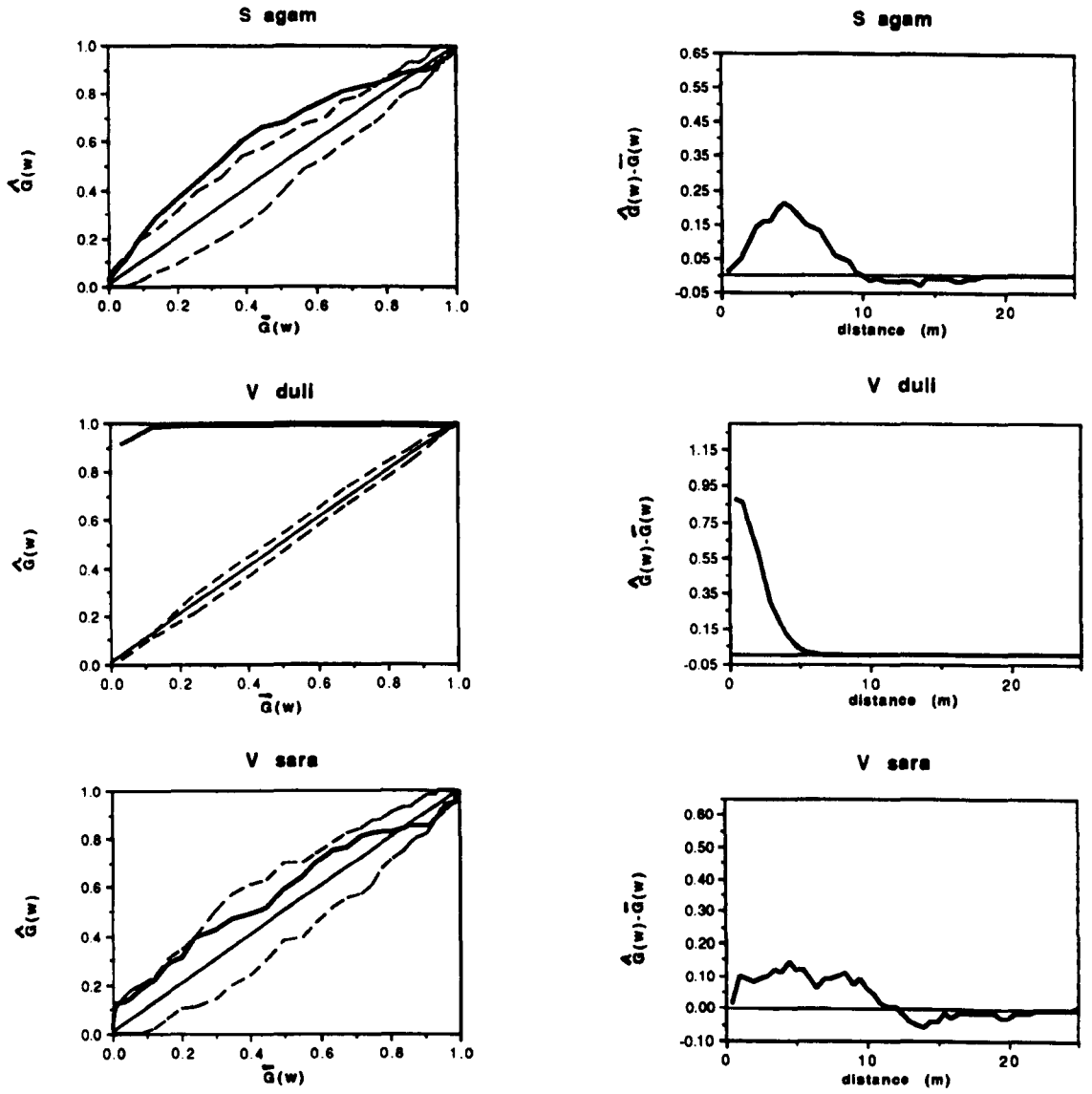


Figure 7.4 (continued) Results of refined nearest-neighbour analysis, G(w), of different species in Plot 1. The first graph of each pair shows the cumulative observed NN distribution $\hat{G}(w)$ (bold line), with mean, $\bar{G}(w)$, and maximum and minimum (dashed lines) G(w) values obtained from 99 random simulations in each species. The second graph of each pair shows $\hat{G}(w)$-$\bar{G}(w)$ plotted against distance (m).

shows that 91.6% of the observed NN distances were less than 0.5 m compared with an expectation of 3.3%. Curves in the remaining species were broadly similar, with maximum difference between $\hat{G}(w)$ and $\tilde{G}(w)$ occurring in the range 2 to 4.5 m.

7.3.4 Second-order analysis, Ripley's $\hat{K}(t)$

Plots of $\hat{K}(t)-\pi t^2$ and $\hat{L}(t)$ against t are shown in Figure 7.5. The value of L_{max} (the maximum difference between $\hat{L}(t)$ and t, the corresponding values of t, and the 1% and 5% significance limits for each species are summarised in Table 7.3. Estimates from the plots of $\hat{K}(t)-\pi t^2$ of the parameters of a Poisson cluster process, together with the observed values, are given in Table 7.4.

Using L_{max} as the test statistic with Ripley's (1979b) significance limits, the test detected significant departure from randomness in six species. In these species, $\hat{L}(t)$ lies above the upper significance limit (Figure 7.5), indicating aggregation at the scale of by t. Randomness was not rejected in the remaining five species, but $\hat{L}(t)$ consistently lay above t for small values of t, indicating a tendency to aggregation in these species. The six aggregated species were three emergent *Shorea* species, *P. malaanonan*, and two canopy species, *H. nervosa* and *V. dulitensis*. The five randomly distributed species were the three remaining emergent *Shorea* species, and two canopy species, *S. agamii* and *V. sarawakensis* (Table 7.3). There was therefore no consistent trend: random and aggregated patterns as detected by $\hat{K}(t)$ analysis occurred in both emergent and canopy species.

In all species the graph of $\hat{K}(t)-\pi t^2$ reached a maximum at values of t less than 50 m. This maximum point gave the estimates of number of adults (or number of patches) and mean squared distance from seedlings to adults (Table 7.4). In the six species with significantly aggregated seedlings, the estimated number of groups (adults) was close to the actual number of adults (Table 7.4). (Adults were defined as trees ≥100 cm gbh and over in emergent species, *Parashorea* and *Shorea* species and ≥80 cm gbh in canopy species, *Vatica* and *Hopea*). Thus, where significant aggregation was detected, the $\hat{K}(t)$ method detects the same number of patches as there were adult trees, suggesting that there is patchiness on the scale of the seedling shadow in these species.

The estimates of mean distance to nearest adult are difficult to compare to the observed values because of edge effects. In calculating distance to nearest conspecific

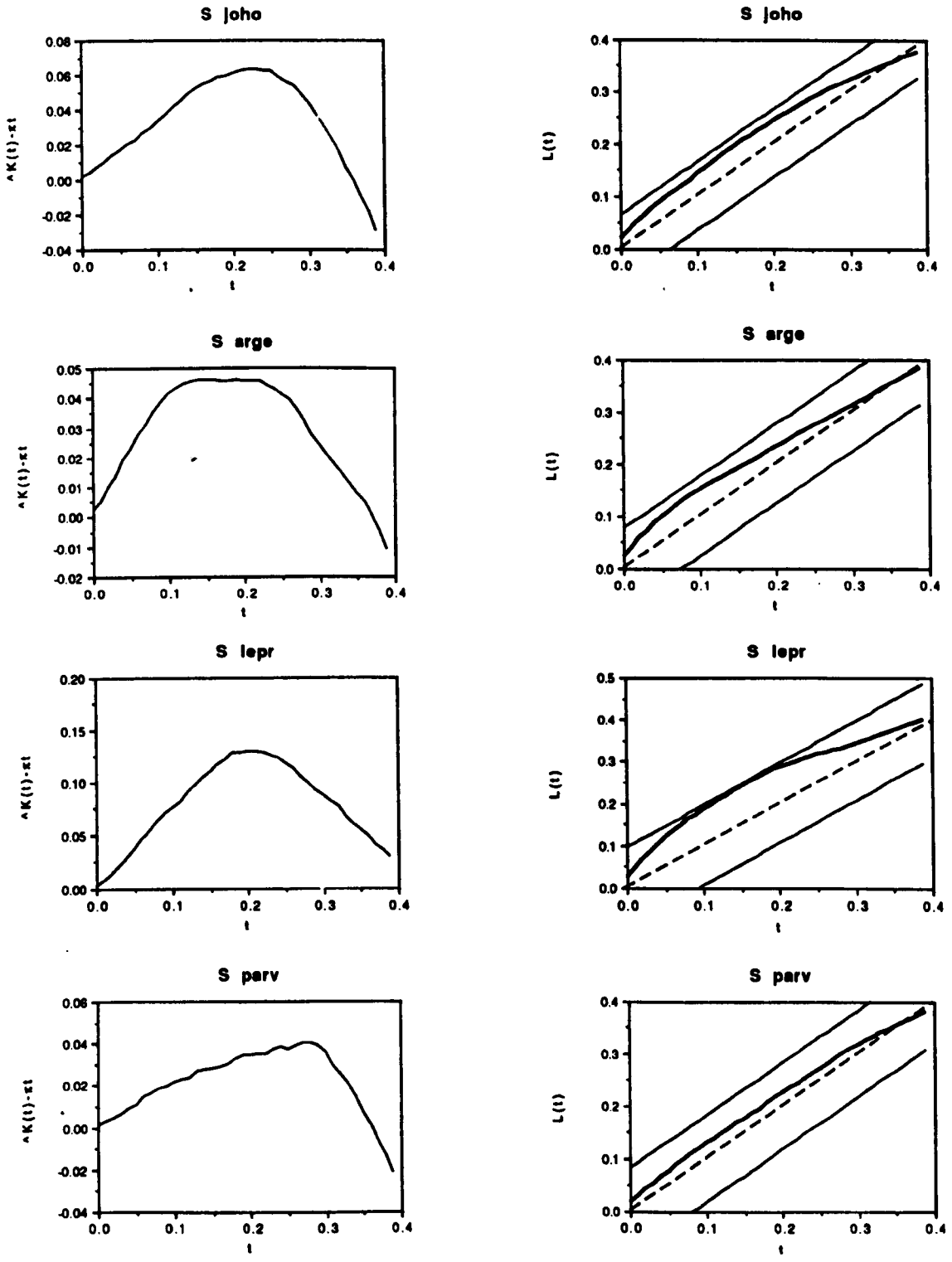


Figure 7.5 Results of second-order analysis, K(t), of seedling spatial patterns. The first graph of each pair shows $\hat{K}(t)-\pi t^2$ plotted against t (distance, m x 10^{-1}). The second graph shows $\hat{L}(t)$ [$=\sqrt{(\hat{K}(t)/\pi)}$] against t, with 1% and 5% significance envelopes.

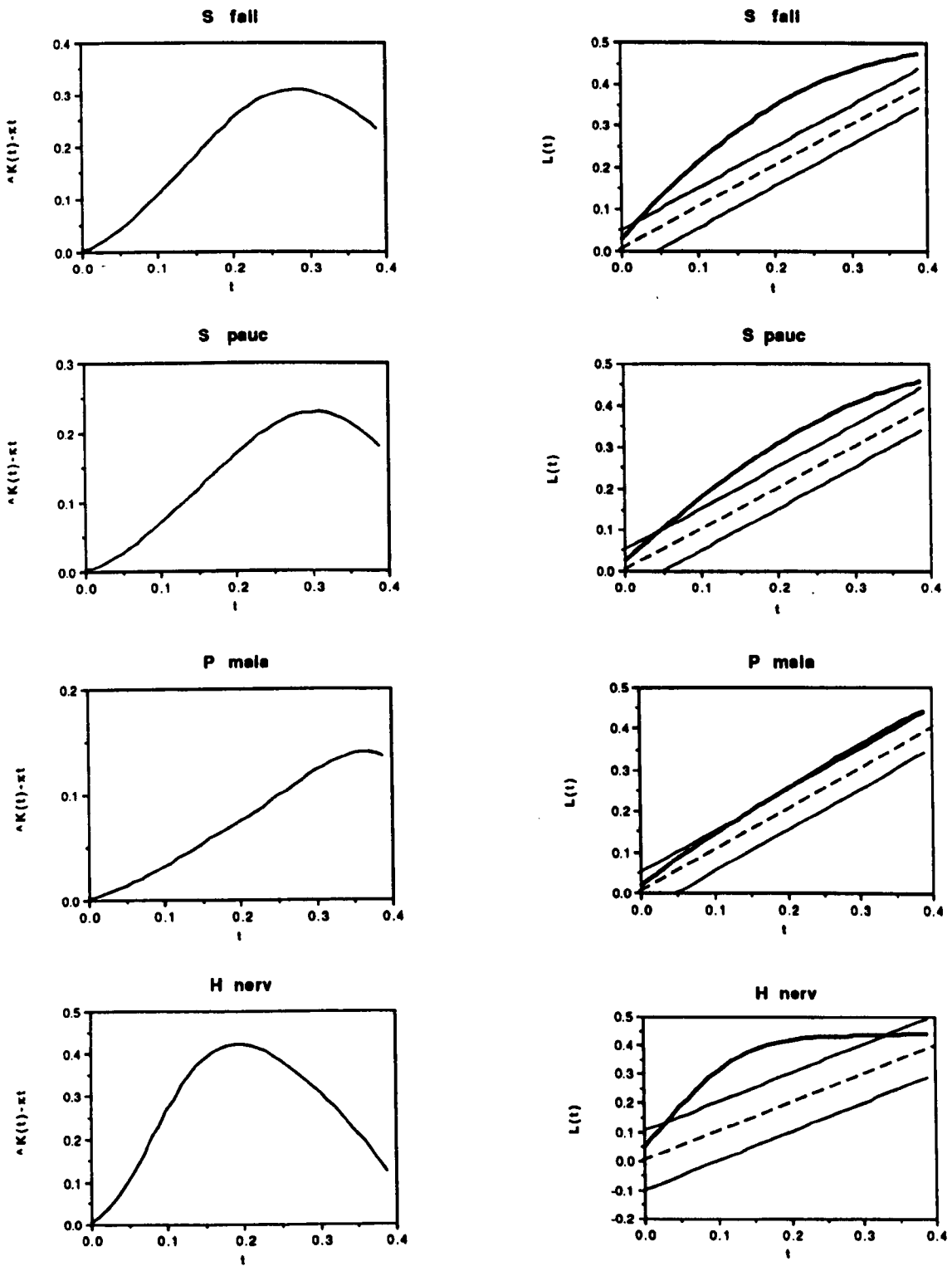


Figure 7.5 (continued) Results of second-order analysis, K(t), of seedling spatial patterns. The first graph of each pair shows $\hat{K}(t)-\pi t^2$ plotted against t (distance, m x 10^{-1}). The second graph shows $\hat{L}(t)$ $[=\sqrt{(\hat{K}(t)/\pi)}]$ against t, with 1% and 5% significance envelopes.

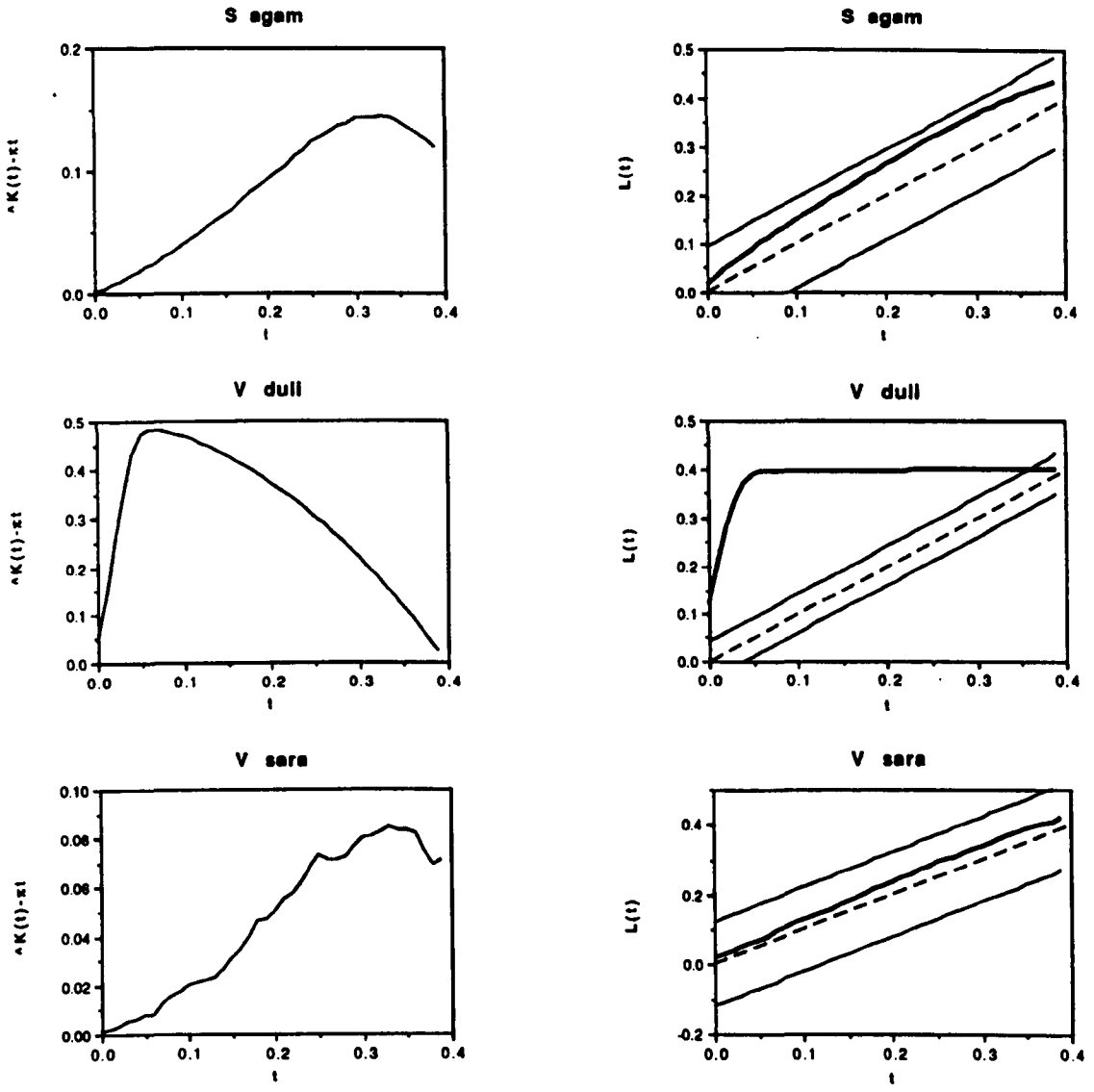


Figure 7.5 (continued) Results of second-order analysis, K(t), of seedling spatial patterns. The first graph of each pair shows $\hat{K}(t)-\pi t^2$ plotted against t (distance, m x 10^{-1}). The second graph shows $\hat{L}(t)$ $[=\sqrt{(\hat{K}(t)/\pi)}]$ against t, with 1% and 5% significance envelopes.

Table 7.3 Results of second-order analysis, $\hat{K}(t)$, of seedling spatial pattern. The value of L_{max}, the maximum difference between $\hat{L}(t)$ and t; the corresponding value of t (in brackets if significant difference from random distribution not detected) and 5% and 1% significance limits, are given for each species in Plot 1.

Species	L_{max}	Value of t at L_{max} (metres)	P	± Limits of $\hat{L}(t)$	
				5 %	1 %
S joho	+ 0.0480	(30)	N.S.	0.0550	0.0651
S arge	+ 0.0527	(18)	N.S.	0.0641	0.0759
S lepr	+ 0.0905	32	*	0.0801	0.0948
S parv	+ 0.0308	(16)	N.S.	0.0695	0.0822
S fall	+ 0.1493	46	**	0.0402	0.0476
S pauc	+ 0.1096	48	**	0.0427	0.0505
P mala	+ 0.0593	62	**	0.0414	0.0490
H nerv	+ 0.2318	30	**	0.0855	0.1011
S agam	+ 0.0694	(54)	N.S.	0.0791	0.0936
V duli	+ 0.3404	12	**	0.0408	0.0345
V sara	+ 0.0429	(50)	N.S.	0.1020	0.1206

Table 7.4 Estimates of the parameters of a Poisson Cluster Process, derived from second-order analysis, Ripley's $\hat{K}(t)$ for each species in Plot 1 (Fig. 7.7). The parameters $1/\varrho$ and 4σ were read from the graph of $\hat{K}(t)-\pi t^2$, and provide estimates of N_{ad}, the number of adult trees, and d, the mean seedling-to-adult distance (metres) respectively. Figures in bold indicate estimates for species detected as significantly aggregated by $\hat{K}(t)$ analysis.

	Max y	t value	Estimates of:		Observed	
Species	(= 1 / ϱ)	(= 4 σ)	N_{ad}	d	N_{ad}	d
S joho	0.063	0.22	15.9	15.6	17	12.2
S arge	0.046	0.15	21.7	10.6	6	23.0
S lepr	**0.130**	**0.20**	**7.7**	**14.5**	5	17.0
S parv	0.040	0.28	25.0	19.8	4	20.6
S fall	**0.310**	**0.28**	**3.2**	**19.8**	3	19.3
S pauc	**0.228**	**0.31**	**4.4**	**21.9**	6	12.6
P mala	**0.140**	**0.37**	**7.2**	**26.2**	4	30.4
H nerv	**0.415**	**0.20**	**2.4**	**14.1**	2	12.9
S agam	0.144	0.33	6.9	23.3	1	28.5
V duli	**0.482**	**0.06**	**2.1**	**4.2**	1	5.1
V sara	0.085	0.33	11.8	23.3	3	26.5

adult, seedlings nearer the plot boundary than to an adult were excluded, whereas in the $\hat{K}(t)$ calculations, all seedlings were included. In the six significantly aggregated species, the estimate of seedling-to-adult distance was within 10% of the calculated value in one species, and within 20% in a further three species. In the remaining two species, the Dark Red Merantis, seedling-to-adult distances were greatly over-estimated.

Despite the assumption of stationarity not being met in the most extremely aggregated species, *V. dulitensis* (which occurred as a single clump), the parameter estimates were very close to the observed values (Table 7.4). The estimated values were two parents, with mean distance to seedlings of 4.2 m, compared to the observed values of one parent and 5.1 m. The mean seedling-to-adult distance could be accurately measured in this species because the clump was distant from the plot boundary, so there were no edge effects. Estimates of patch diameter were 15 m in *V. dulitensis*, and ranged from 41 m to 54 m in the other aggregated species (Table 7.3).

7.4 PATTERN OF DIPTEROCARP TREES

Patterns of trees (≥10 cm gbh) in the two 4 ha plots were analysed with the Clark-Evans test and Morisita's Index. In each plot, only species with seedlings in the seedling study area of that plot were analysed. Only species with more than four trees were included.

7.4.1 Results

7.4.1.1 Variation between species

Results of the Clark-Evans test are given in Table 7.5. In Plot 1, eight out of eleven species were significantly aggregated, and in Plot 2, six out of nine. No species were significantly regularly distributed, though in *V. sarawakensis* in Plot 1, the observed NN distance was less than expected. In Plot 1, distribution patterns of *H. nervosa*, *S. agamii* and *V. sarawakensis* were indistinguishable from random. These are

Table 7.5 Results of the Clark-Evans test of tree (≥10cm gbh) spatial distribution in Plots 1 and 2 (4 ha). Species are included only if their seedlings were present in the seedling study area within the same plot. E(W) and w are the expected and observed mean nearest-neighbour distances, var(W), the variance and R, the ration w/E(W). Absolute values of the test statistic CE, the standard normal deviate, exceeding 1.645 indicate significant departure from randomness at the 5% level, (*); CE >2.33, the 1% level (**), and CE >3.11, the 0.1% level (***).

(a) Plot 1

Species	N	w	E(W)	var(W)	R	CE
S joho	111	8.08	9.99	0.285	0.81	-3.57 ***
S arge	34	15.36	18.86	3.530	0.82	-1.86 *
S lepr	47	10.86	15.80	1.762	0.69	-3.72 ***
S parv	97	9.02	10.72	0.379	0.84	-2.76 **
S fall	189	4.56	7.56	0.094	0.60	-9.80 ***
S pauc	87	9.43	11.36	0.476	0.83	-2.79 **
P mala	71	10.00	12.66	0.732	0.79	-3.10 **
H nerv	6	36.10	52.18	162.029	0.69	-1.26
S agam	8	39.49	43.59	84.817	0.91	-0.44
V duli	7	26.24	47.35	114.468	0.55	-1.97 *
V sara	15	36.48	29.94	20.990	1.22	+1.43

(b) Plot 2

S joho	86	7.92	11.43	0.488	0.69	-5.03 ***
S arge	46	16.03	15.99	1.845	1.00	0.03
S lepr	13	20.28	32.55	28.783	0.62	-2.29 *
S parv	108	9.39	10.13	0.302	0.93	-1.35
S fall	178	6.77	7.80	0.106	0.87	-3.16 ***
P mala	79	9.01	11.96	0.584	0.75	-3.83 ***
H nerv	93	6.59	10.96	0.414	0.60	-6.80 ***
S pilo	109	5.58	10.08	0.296	0.55	-8.27 ***
V sara	16	26.38	28.84	18.211	0.92	-0.58

all canopy species, each with fewer than 15 trees. In Plot 2, two canopy species, *S. symingtonii* and *V. sarawakensis*, and two emergent species, *S. parvifolia* and *S. argentifolia* were randomly distributed.

Values of Morisita's Index for different species in Plots 1 and 2 are shown in Fig 7.6. In most species, I_m values were greater than 1.0 for most quadrat sizes, and showed a consistent exponential decrease in I_m values with increasing quadrat size, typical of a clumped distribution with density decreasing exponentially from the centre of the clump outwards (Hubbell 1980). In other species, notably *S. pilosa* in Plot 2, I_m values rose initially at small quadrat sizes, then decreased, suggesting that, while the population is clumped, the within-clump distribution of individuals tends to be regular. A further pattern is seen in *S. fallax* in both plots, where I_m remained constant at small quadrat sizes, before decreasing, suggesting that trees within the clumps are randomly dispersed. Index values for *P. malaanonan* are closely similar in the two plots, and show a decrease in I_m value for quadrat sizes around 7 m, though I_m values are not much higher than 1.0 in either plot, indicating population distributions close to random. *S. parvifolia* and *S. argentifolia* also have very similar I_m values in both plots.

7.4.1.2 Pattern of all trees

The plots of I_m values for all species pooled (Figure 7.7) show that, in total, dipterocarps in both plots were weakly clumped. Index values for the two plots were closely parallel at quadrat sizes greater than around seven metres, with the values for Plot 2 slightly higher. Below seven metres, index values in Plot 2 continued to rise, while in Plot 1, they fell. This suggests a tendency to regular spacing within dipterocarp clumps in Plot 1. However, the Index values are quite similar, suggesting no great difference in the general distributions of dipterocarp between plots.

I_m values for progressively larger trees (<30 cm, ≥60 cm, ≥120 cm gbh) are plotted in Figure 7.7. As tree size increases, Index values decrease, indicating that larger trees tend to be less clumped than smaller trees. Large trees tend to be regularly spaced (I_m is less than one) at small quadrat sizes, particularly in Plot 2. This is likely to be a consequence of 'space-filling' - there will be some degree of repulsion at small spatial scales between large trees with crowns in the main canopy.

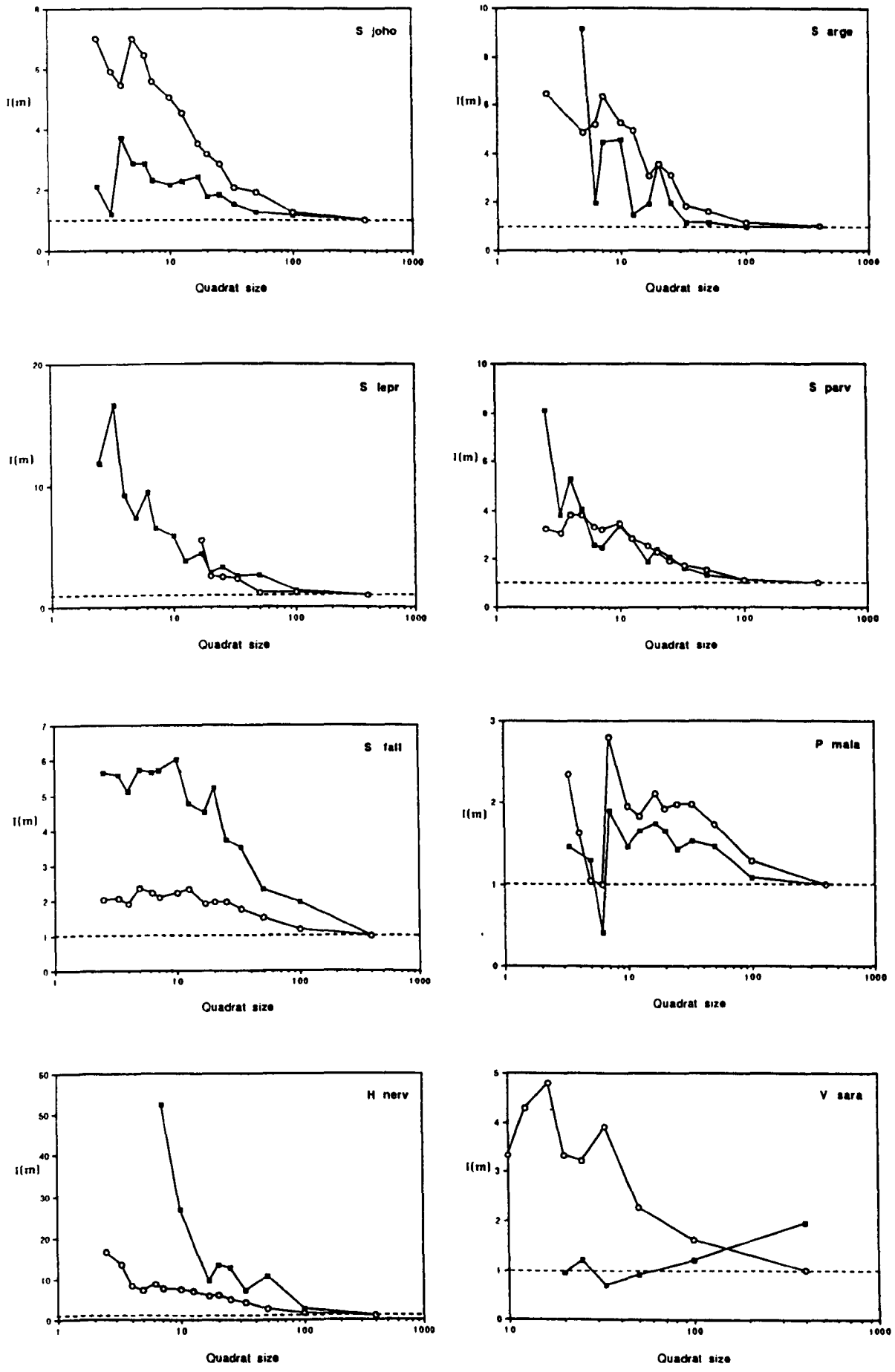
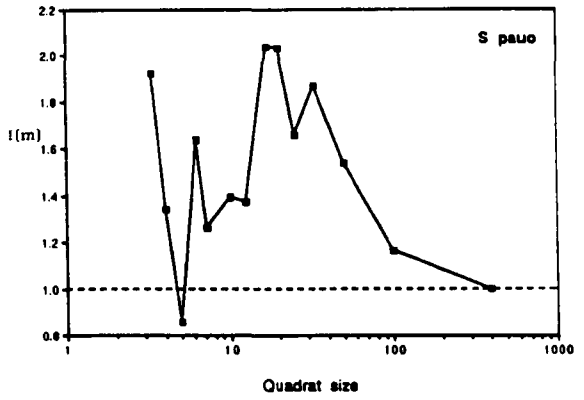
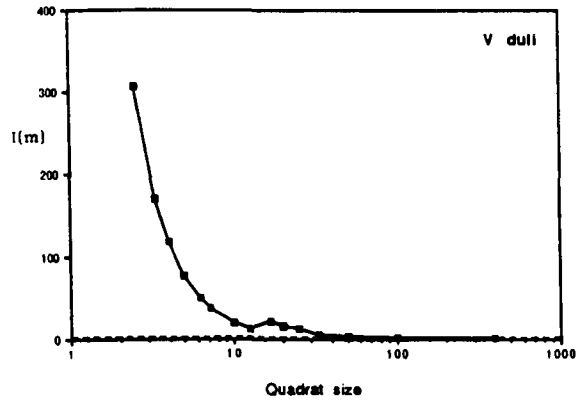


Figure 7.6 Values of Morisita's Index, I_m, in a range of quadrat sizes (side length, m) in different species of dipterocarp tree (≥10cm gbh) in Plots 1 (■) and 2 (O). The dashed line at I_m=1.0 is the Index value for a random distribution.





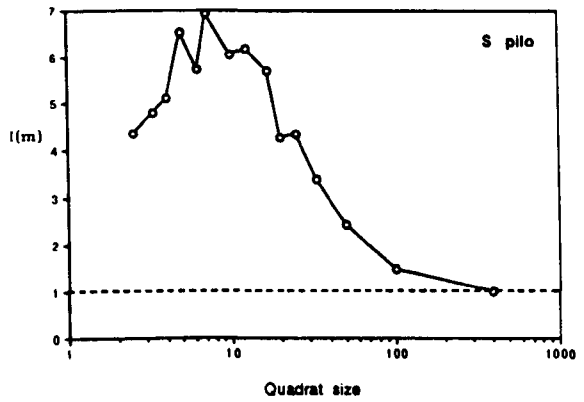


Figure 7.6 (continued) Values of Morisita's Index, I_m, in a range of quadrat sizes (side length, m) in different species of dipterocarp tree (≥10cm gbh) in Plots 1 (■) and 2 (O). The dashed line at I_m=1.0 is the Index value for a random distribution.

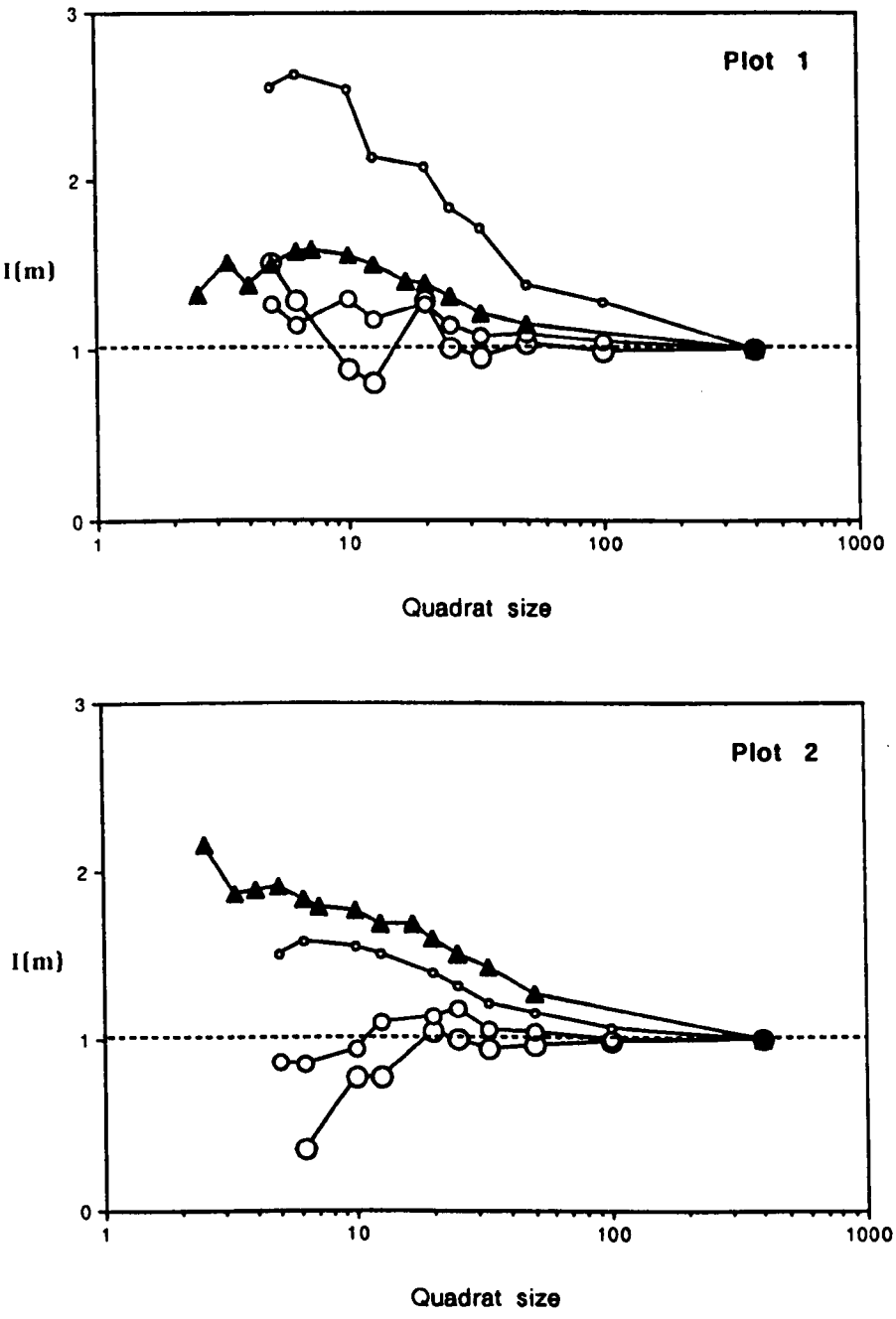


Figure 7.7 Values of Morisita's Index, I_m, in a range of quadrat sizes (side length, m) for dipterocarp trees of all species pooled, in Plots 1 and 2 (4 ha area). The dashed line at I_m=1.0 is the Index value for a random distribution. Three different size classes are illustrated: ○, trees ≥120 cm gbh; O, trees ≥60 cm gbh; ∘, trees <30 cm gbh; and ▲, all trees ≥10 cm gbh.

7.4.2 Comparison of seedling and tree patterns

Are adults less clumped than seedlings of the same species? Do species with less clumped seedlings also have less clumped adults? The fact that trees are less clumped than adults provides indirect evidence for some form of spacing mechanism (Clark & Clark 1984, Sterner *et al.* 1986). The value of the Clark-Evans test statistic, CE, was used as a measure of the strength of departure from randomness to compare seedling and adult patterns. In all of the eleven species in Plot 1 trees were less aggregated than seedlings of the same species (Figure 7.8). The situation was different in Plot 2 - here seedlings were more clumped in only five out of nine species. This may be partly an effect of the small size of seedling populations in the 0.48 ha study area, and the difference in scale between the adult and seedling tests (adults were tested in 4 ha main plot). *H. nervosa*, which had strongly aggregated seedlings, did not have significantly clumped trees in Plot 1, but numbers were low (N=6), leading to very high variance term. The ratio R was one of the lowest. As with seedlings, the trees of the two *Vatica* species were at opposite ends of the range if species are ranked by the value of R. In trees of *V. sarawakensis*, observed NN distance was actually greater than expected, indicating a degree of hyper-dispersion, though it did not reach significance. Seedlings of all the emergent species in Plot 1 were strongly clumped ($P<0.001$), but trees of *S. argentifolia* were clumped at 5% level of significance, and those of three other species at the 1% level. In Plot 2, *S. argentifolia* and *S. parvifolia* trees were randomly dispersed - these were the two dominant emergent trees over much of the Plot. Large girth trees (>120 cm gbh) showed a tendency to uniformity, especially in Plot 2.

Morisita's Index values for trees showed peaks in light-demanding species, the LRMs, *S. johorensis* and *P. malaanonan*, which could indicate (bearing in mind Hurlbert's [1990] reservations) that trees were clumped at a scale of 7-10 m. Combined with the observation that large seedlings in these species (>250 cm tall to <10 cm gbh) were more clumped than small seedlings (≤1 m tall), this suggests that clumping in these species may be at the scale of small canopy openings. (10 m is too small to be seedling shadow remnant pattern).

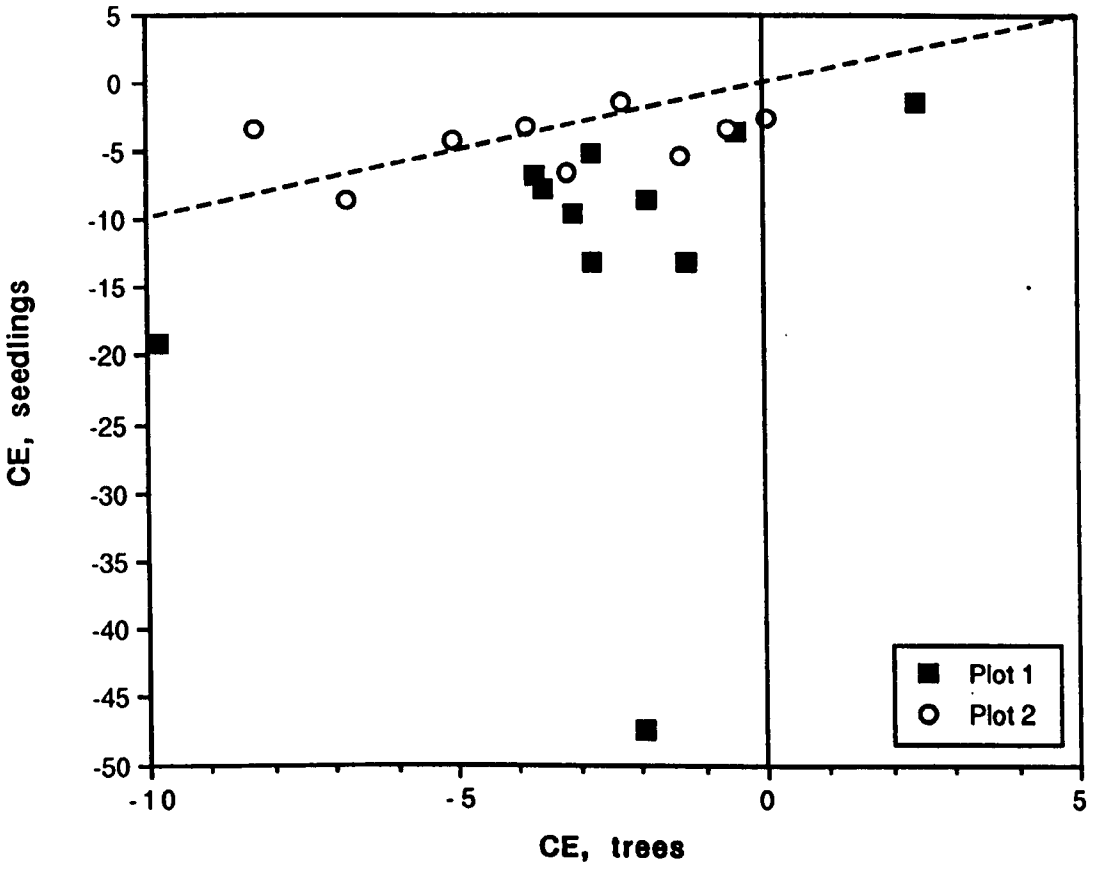


Figure 7.8 Comparison of the Clark-Evans test statistic, CE, for spatial pattern of trees and seedlings in different species in Plots 1 and 2. Dashed line shows equal value of the test statistic in trees and seedlings.

7.5 DISCUSSION

When interpreting spatial patterns, it is important to look at maps of species distributions (Hurlbert 1990) (given in Appendix 3). Obvious changes in intensity across the plot can be seen, and borne in mind when interpreting test results (Ripley 1981). Other aspects of pattern, such as the number of patches, may not be so easily discernible (Diggle 1983). Size variation of individuals within patches provides additional information and could help distinguish true contagion from environmental heterogeneity.

Comparison of test results

Four tests were used to explore different aspects of seedling pattern in 11 species in Plot 1. The Clark-Evans test provided an initial quick test of departure from randomness, based on mean nearest-neighbour distance. This was extended to look at the distribution of all nearest-neighbour distances in refined nearest-neighbour analysis, G(w). The quadrat-based method, Morisita's Index, showed how pattern varied with scale, but did not provide a satisfactory formal test of departure from randomness. Second-order analysis, Ripley's K(t) function, considered all inter-plant distances and combined significance testing with information on variation in pattern with distance. Results are summarised in Table 7.6. How consistent were the results from these four tests?

All four tests agreed on acceptance of randomness in *V. sarawakensis*. Detection of aggregation is in part a function of population size in some quadrat-based tests (Greig-Smith 1983), and in the Clark-Evans test, small population size often results in a large variance term, reducing the value of the test statistic CE. As a result, rare species are often detected as random (Greig-Smith 1983). *V. sarawakensis* had the smallest population size (N=97) of the species tested in Plot 1, but the value of R (ratio of w:E(W), the ratio of observed to expected nearest neighbour distances), which is unaffected by sample size, was also the lowest. *V. sarawakensis* was ranked least, or second least, aggregated in all the tests. In Plot 2, *S. leprosula* illustrates this point: few seedlings were present (N=18), and the Clark-Evans test failed to detect aggregation, although the value of R was not the lowest. All the tests agreed that *V. dulitensis* was the most strongly aggregated

Table 7.6 Summary of results of different tests of seedling spatial distribution in Plot 1: CE, the Clark-Evans test statistic (based on mean nearest-neighbour distance); I_m, the value of Morisita's Index at quadrat sides of length 10 m and 50 m; L_{max}, the maximum difference between observed $\hat{L}(t)$ and expected $L(t)$ in second order analysis, Ripley's $K(t)$; d_w, the maximum difference between $\hat{G}(w)$ and $\bar{G}(w)$ in refined nearest neighbour analysis. Values for test statistics are given in brackets if the test failed to detect departure from randomness. Figures in bold give the rank order of each species in the each test.

Species	CE		I_m * 10m		I_m * 50m		L_{max}		d_{max}	
S joho	-7.682	5	2.85	5	1.33	3	(+0.048)	3	0.286	5
S arge	-8.610	6	3.31	6	1.43	4	(+0.053)	4	0.338	6
S lepr	-6.826	4	4.92	9	2.42	7	+0.090	7	0.349	7
S parv	-5.119	3	1.93	2	1.21	1	(+0.031)	1	0.176	2
S fall	-19.210	10	4.79	8	2.85	9	+0.149	9	0.445	9
S pauc	-13.160	9	3.24	7	2.46	8	+0.110	8	0.362	8
P mala	-9.560	7	2.03	3	1.53	5	+0.059	5	0.233	4
H nerv	-13.040	8	11.07	10	4.37	10	+0.232	10	0.621	10
S agam	-3.560	2	2.28	4	1.56	6	(+0.069)	6	0.261	3
V duli	-47.450	11	23.62	11	9.37	11	+0.340	11	0.883	11
V sara	(-1.300)	1	1.63	1	1.25	2	(+0.043)	2	(0.142)	1

* significance testing was not performed on I_m results

species. *H. nervosa* and the two Dark Red Merantis, *S. fallax* and *S. pauciflora* were ranked eighth to tenth in most tests. Rankings of the remaining species were less consistent between tests.

Results from second order analysis, Ripley's $\hat{K}(t)$ analysis differed from the two tests based on nearest-neighbour distances in the failure to detect significant aggregation in four species: *S. johorensis, S. argentifolia, S. parvifolia* and *S. agamii*. $K(t)$ considers all inter-plant distances, and may therefore be less sensitive to departures from randomness which occur at very small distances. By shifting the focus from the smallest distances between neighbouring seedlings to all interplant distances, the larger-scale patterns also influence the test results. These four species are relatively well distributed throughout the two hectares, and the inter-plant distances at this larger scale were therefore not different from expectation. This is confirmed by the behaviour of Morisita's index, I_m, in these species in quadrats of side 33.3 m, 50 m and 100 m. I_m values for these four species were among the lowest of all species, and were around 1.0, indicating that the dispersion of seedlings in larger quadrats was essentially random. The rankings of species by the degree of aggregation detected by $\hat{K}(t)$ analysis were identical to their ranks by I_m values for quadrats of side 50 m. However, nearest neighbour distances in these species were still significantly smaller than expected, and I_m values were highest in the smallest quadrat size (2.5 m). The picture that emerges in these species is of generally well-distributed seedlings throughout the 2 ha plot, with some degree of aggregation at very small scales.

In summary, the four tests gave reasonably consistent results. One interesting point from these analyses is that the simple tests (Clark-Evans test and Morisita's Index) gave results very similar, and sometimes identical, to the potentially more informative and computationally more expensive methods. Specifically, ranking of species by the I_m values for 50 m quadrats was identical to their ranking in the $\hat{K}(t)$ analysis, and rankings in Clark-Evans test and refined nearest neighbour analysis were very similar.

Parameter estimation from $\hat{K}(t)$ analysis

Significant aggregation was detected by $\hat{K}(t)$ analysis in six species. Estimates of the parameters of a simple Poisson cluster process gave values for the number of adults that were very similar to the observed number of adults in five of the six

species. This suggests that in these species, seedlings are aggregated at the scale of the seedling shadow (Hubbell 1979). It further suggests that a simple Poisson cluster model, in which the number of seedlings per adult follows a Poisson distribution and seedlings are distributed relative to the adults in a radially symmetric normal distribution (Diggle 1979), may fit the observed seedling distributions in these species. This model has been fitted to seedlings of redwood (Diggle 1983) clustered around stumps whose positions were unknown (Strauss 1975). In the present study, the position of adults was known, and estimates of mean seedling-to-adult distances in the species detected as aggregated also closely matched the observed (edge-corrected) distances.

Variation between species

Seedling spatial patterns in the eleven species tested covered a wide range of degrees of aggregation, from complete randomness to highly aggregated: in *V. dulitensis*, the mean observed nearest neighbour distance was almost a tenth of expected distance. The three canopy species had very different patterns: the two *Vatica* species were the extreme ends of the range. *H. nervosa* was one of the most aggregated species. The two Dark Red Merantis had very similar patterns, both being strongly aggregated. The Light Red Merantis, *S. johorensis* and *P. malaanonan* were less aggregated than the DRMs. Ranking of LRMs and *P. malaanonan* were less consistent between the four tests than the rankings of DRMs, suggesting that pattern varied more with scale in LRMs. On a larger scale, these species were generally well-distributed throughout the plot, but with a degree of aggregation at small scales. There was evidence from Morisita's Index that larger seedlings (>250 cm tall) were more clumped than small seedlings in the LRMs. Taken together these results suggest that the original seedling shadow pattern has been weakened by high seedling mortality since the last mast-fruiting (>4 yr before study started), and a secondary pattern of small-scale clumping is due to enhanced survival and growth in small canopy gaps. There was some evidence from Morisita's Index that seedlings of the two Meranti groups were distributed in non-overlapping patches.

Other studies have recorded differences in spacing of different species of dipterocarp trees. Fox (1972) describes the patterns of different species in several different forest types. At Segaliud-Lokan, near Sandakan, north Sabah, he notes that

the major species are often grouped at the scale of less than a hectare, but *Parashorea tomentella* (closely related to *P. malaanonan*) was well-scattered. At Kalabakan, four square miles were sampled with 63 x 0.4 ha plots - trees of all dipterocarp species were aggregated except *S. parvifolia*. The order of aggregation (most to least) was *S. pauciflora, S. johorensis, S. leprosula*, and *S. parvifolia*. This is identical to the order of aggregation of seedlings in Plot 1. Though trees in Plot 1 differed, trees in Plot 2 were ranked in the same order as at Kalabakan, though *S. pauciflora* was absent. At Pasoh, Chan (1980) found four dipterocarp species to be clumped, including *S. leprosula*, but that *S. parvifolia* was not. Poore (1968) noted that large (>91 cm gbh) trees of both *S. leprosula* and *S. parvifolia* were randomly distributed, while *Hopea* species are commonly clumped. Trees of *S. parvifolia* were randomly distributed in Plot 2, and clumped in Plot 1. Seedlings of *S. parvifolia* were not distinguished from random in the $\hat{K}(t)$ test, were the second least aggregated in both the refined nearest neighbour analysis, $\hat{G}(w)$, and in Morisita's Index, and was the third least aggregated in Clark-Evans test.

Clumping of adult trees has significance for breeding biology and is a determinant of effective population size (Poore 1968). In clumped species, gene transfer may be restricted largely to within the clump, whereas in more randomly dispersed species, gene flow over longer distances may be possible. Ashton (1969) suggests that the combination of limited pollen transfer and inefficient seed dispersal help to reinforce the group as the breeding unit.

Are adults less clumped than seedlings?

The fact that adults trees are less clumped than seedlings may provide indirect evidence for some form of spacing mechanism (Clark & Clark 1984). In Plot 1, trees were less clumped than their seedlings in all eleven species. Similar trends of increasing spacing with increasing size have been found in other studies. Sterner *et al.* (1986) in Costa Rica found that in three out of four species studied, larger trees were more uniformly dispersed than small trees. In dry forest in Costa Rica, Hubbell (1979) found that adults were less clumped than juveniles in half of the 30 commonest species. When all species were combined in the Danum Study, there was a similar increase in spacing with increasing size (Figure 7.7). Lieberman & Lieberman (in press) obtained similar results at La Selva, Costa Rica: trees in the canopy (>40 cm dbh) were more regularly spaced than trees in the understorey (<40 cm dbh), both in

a single species, *Pentaclethra macroloba*, the dominant large tree species, and in all species pooled. Since the Janzen-Connell mechanisms are host-specific, they conclude that Janzen-Connell spacing cannot be inferred, since the pattern of all species pooled cannot be distinguished from that of individual species, and suggest physical crowding and crown-crown interactions of neighbouring trees as a more parsimonious explanation. Both Ashton (1969) and Poore (1968) found that large girth trees in Malaysian dipterocarp forests were random or clumped, almost never uniformly distributed.

CHAPTER 8

SPATIAL RELATIONSHIPS BETWEEN SEEDLINGS AND TREES

8.1 INTRODUCTION

Differences exist between species in seedling density, number of adult trees in the population (Chapter 2) and in tree and seedling spatial pattern (Chapter 7). These three factors and their interactions are complex and have implications for local density of seedlings, seedling mortality and growth patterns, and seedling dispersion relative to adult trees. Ultimately, these will influence recruitment and replacement processes.

Seedling dispersion patterns can be viewed from three angles. The individual seedling's chance of survival (Chapter 3.6) and its growth rate (Chapter 4.10) were affected by proximity to the nearest large tree in some species. The dispersion pattern of the whole seedling population will determine local seedling density. The chance of a seedling encountering a newly created canopy gap is dependent partly on the spatial distribution of the seedling population, and is likely to be higher if seedlings are well-dispersed than if they are strongly clumped. Finally, from the point of view of the adult tree, the dispersion pattern of its seedlings will determine the chance of replacement at the same site.

8.2 SEED DISPERSAL AND SEEDLING DISPERSION

The efficiency of seed dispersal determines the initial pattern of seedlings. Mechanisms causing differential mortality and growth act upon the original

distribution to produce the observed pattern of seedlings, representing, in the dipterocarps, the survivors of several cohorts over many years.

Differences between species in the dispersibility of fruit may, in part, help to explain the currently observed seedling dispersion patterns. Because a mast-fruiting event could not be studied directly, inferences on dispersibility must be drawn from other sources. Two aspects of variation in dispersibility between species were investigated. Firstly, variation between species in fruit morphology were explored, and secondly, the variations between juvenile and adult dispersions were compared.

8.2.1 Fruit morphology

Mature dipterocarp fruit have elongated sepals attached to the nut, which allow the fruit to spin as it descends, slowing the rate of descent, and thereby increasing the chance of wind dispersal. Within the canopy, elongated wings are not advantageous; as there is little wind the fruit fall vertically and can become trapped in branches and die (Chan 1980). Thus there is a trade-off between short and long sepals, and some species have re-evolved shorter sepals (Ashton 1988a). Understorey and canopy species such as *V. sarawakensis* and *V. dulitensis* have very short wings. Dipterocarp fruit have been observed to disperse over large distances (up to 1/2 mile in gusty winds (Webber 1934, Poore 1968), but such observations are rare. Most reports emphasise the limited efficiency of dispersal, the majority of fruit falling close to the parent tree (Ridley 1930, Poore 1968, Fox 1972, 1973, Liew & Wong 1973, Kochumman 1978, Chan 1980, Ashton 1982).

Potential dispersal distance of propagules is inversely related to rate of descent of the fruit (Augspurger 1986). Rate of descent has been shown to be highly correlated with square root of wing-loading, defined as seed weight divided by wing-area, in seven species of temperate tree (Green 1980). Augspurger (1986) postulates that rate of descent is related to light-demanding status: species requiring light gaps for regeneration will have a slow rate of descent to enable far dispersal, thereby increasing the chance of encountering a gap. Seed size may be related to the ability of seedlings to establish in gaps or in closed forest (Swaine & Whitmore 1988). Fox (1972, 1973) distinguishes four groups of dipterocarps in Sabah, based on their fruit wing length to weight ratio and seedling dispersion pattern, and suggests that

wing area and weight are important in seed distribution.

To examine the relationship between fruit morphology, potential dispersal distance and seedling dispersion pattern in different species, I derived an index of wing loading and attempted to relate this to the observed distribution of seedlings relative to adults.

8.2.2 Variation in seedling and tree dispersion

Variation in the dispersion patterns of trees and seedlings was compared using the method of Streng *et al.* (1982). If different species have similar effectiveness of seed dispersal, there should be a positive linear relationship between the variation in numbers of seedlings and adult trees between subplots (Streng *et al.* 1982). Species with widespread adults should have widespread seedlings, while species with aggregated adults should have aggregated seedlings. The analysis makes no assumptions about, and gives no information on, the relative spatial positions of adults and seedlings. Clumping of seedlings could arise for reasons unconnected with seed dispersal patterns, for example due to edaphic factors.

8.2.3 Methods

Fruit dimensions

There was virtually no fruiting of dipterocarps around the study area between 1985 and 1988, so direct measurements of weight, wing area and rate of descent could not be made on fresh fruit. Nut volume and wing area were derived from fruit dimensions given by Ashton (1982) and used to calculate an index of wing-loading. For the same reasons, dispersal distances of fruit could not be measured, so the patterns of existing seedlings were examined instead, since these are the result of more recent dispersal episodes.

The fruit wings were assumed to be ellipses of length l, and breadth b, and the area of each was calculated as $(\pi lb)/6$. The areas of each wing (in *Shorea* species usually two large and three small wings) were summed to give an estimate of total wing area (TWA) for a typical fruit. The nuts are spherical to ovoid in shape (Ashton

1982). Nuts of the *Vatica* species were treated as spheres of diameter d. Nuts in the other genera are more ovoid (Meijer & Wood 1964, Ashton 1983), and were treated as oblate spheroids (Wright & Howe 1987), with volume (NV) estimated from $(\pi d^2 h)/6$, where h is the longest dimension of the nut, and d the diameter. The wing loading index (WLI) was obtained from $WLI = \sqrt{(NV/TWA)}$. Comparison was made between species, assuming that nuts of different species have similar densities.

Variation in seedling and tree dispersion

Variation in numbers of seedlings and adult trees in 20 x 20 m subplots can be estimated by the coefficient of variation, CV (Streng *et al.* 1982). The CV of seedling numbers in the subplots was regressed on the CV of numbers of adult trees in the same subplots for each species. Points lying above the line indicate species with poorer seedling dispersibility relative to the other species, and points below the line species with better dispersibility. The residuals then give an estimate of differences between species in dispersibility (Streng *et al.* 1982). Eleven species had sufficient numbers of trees to test.

8.2.4 Results

Fruit dimensions

Estimated fruit dimensions and wing loading index are given in Table 8.1. Both nut volume and wing area varied between species by a factor of 30 times. Largest nut was in *V. sarawakensis*, and the smallest in *V. dulitensis*. Wing area was lowest in *V. sarawakensis* and highest in *P. malaanonan*. Values of WLI varied by a factor of 15, and were highest in *V. sarawakensis* and lowest in *S. parvifolia*. Potential dispersal distance is inversely related to WLI, so a lower values of WLI indicates dispersal of seed to longer distances.

Variation in seedling and tree dispersion

The relationship between the CVs of seedling and adult tree numbers in eleven species in Plot 1 is shown in Figure 8.1. There was a significant relationship between CV of adult numbers and CV of seedling numbers (Figure 8.1, $r^2=0.29$, n=11, P=0.05). Residuals from the regression are given in Table 8.1, together with the proportion of

Table 8.1 Estimates of wing area (WA), nut volume (NV), index of wing-loading (WLI), residuals from regression of the co-efficient of variation, CV, of seedling dispersion against CV of tree dispersion (Figure 8.1; see text for details), and percentage of 20x20 m sub-plots containing seedlings and trees of different species in Plot 1.

Species	Estimates of wing area (cm^2)	Estimates of nut volume (cm^3)	WLI= $\sqrt{NV/WA}$	CV residual	% occupied 20x20m sub-plots: seedlings	% occupied 20x20m sub-plots: trees ≥ 30 cm gbh
S joho	47.4	2.05	0.21	-0.03	94	74
S arge	14.4	0.59	0.20	-0.35	86	18
S lepr	33.1	1.77	0.23	0.69	74	44
S parv	21.9	0.36	0.13	-0.18	90	64
S fall	6.7	1.41	0.46	0.48	66	42
S pauc	23.8	1.06	0.21	0.23	80	50
P mala	50.1	1.74	0.19	-0.52	86	30
H nerv	25.0	0.52	0.14	0.45	28	4
S agam	40.2	2.36	0.24	-2.18	66	2
V duli	2.9	0.27	0.31	2.54	10	2
V sara	1.8	8.18	2.13	-1.03	76	6

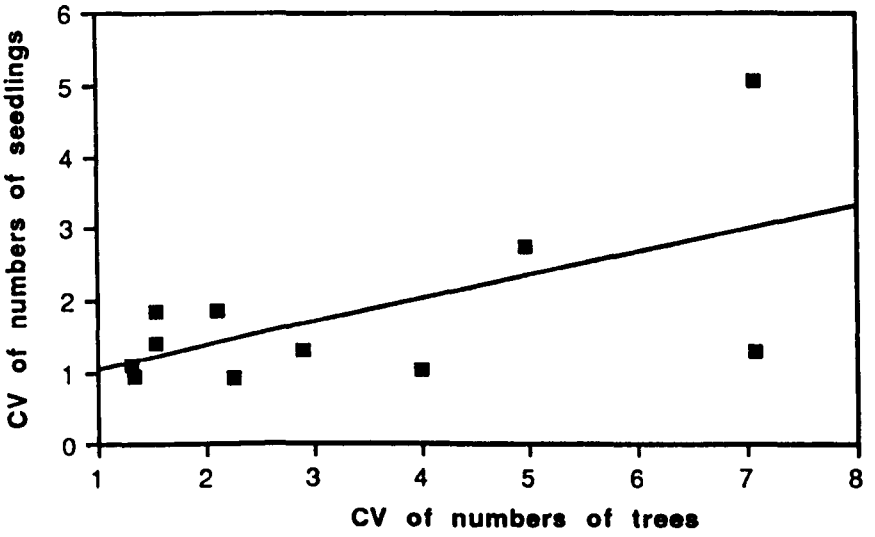


Figure 8.1 Relationship between the coefficients of variation, CV, of numbers of seedlings and numbers of trees over 30 cm gbh in 20 x 20 m subplots in Plot 1. Regression is significant ($P<0.05$).

20 x 20 m subplots occupied by seedlings and adults of each species. Negative residuals indicate species whose seedlings are well dispersed relative to other species, while positive residuals indicate relatively poorer seedling dispersion. In general, the emergent *Shorea* species had low CVs for both seedlings and adults - these were species with both numerous adults and relatively abundant seedlings. *S. argentifolia*, *S. parvifolia* and *P. malaanonan*, among the emergent species, and *V. sarawakensis* and *S. agamii* (canopy species) lay below the line, indicating well-dispersed seedlings. Points for *S. pauciflora*, *S. fallax* (emergent species), *H. nervosa* and *V. dulitensis* (canopy species) lay below the line, indicating more limited dispersal. There was no relationship between either WLI or nut volume and the residual of the regression of CVs for adult and seedling numbers (Spearman r_s=0.08 and 0.527 respectively; n=11 p>0.05). The two species with the largest nuts, *V. sarawakensis* and *S. agamii*, had relatively well-dispersed seedlings (Table 8.1). The emergent *Shorea* species all had similar values of WLI and CV residuals.

8.3 THE RELATIVE DISPERSION OF SEEDLINGS AND TREES

8.3.1 Introduction

Limited seed dispersal in dipterocarps results in high numbers of seedlings near the seed-parent (Poore 1968, Fox 1972, 1973, Chan 1980, Ashton 1982). Even if mortality is higher near the parent (Chapter 3.6), and only a small proportion of these seedlings survive, density is still likely to remain higher near the parent (Hubbell 1980, Augspurger 1983a, Clark & Clark 1984). Therefore, numbers of seedlings give a better picture of recruitment probabilities than density, because recruits are more likely where seedling numbers, rather than densities, are highest, and seedlings further from the adults appear to be a smaller proportion of the population if density rather than numbers is used (Becker *et al.* 1985). The species composition and size structure of the seedling around each adult tree will influence recruitment processes, and ultimately, the species identity of the replacing tree (Hubbell & Foster 1987). It is therefore important to quantify the 'demographic neighbourhood' (*sensu* Hubbell

1979) in terms of species composition, seedling numbers and density, and population size structure with respect to the specific identity of the adult, and to quantify changes in composition and density with increasing distance from the adults.

The aim of this section is to describe seedling dispersion relative to adult trees in each species. Firstly, single species patterns are examined: the relationship between adults and conspecific seedlings. Variation in seedling numbers and density with distance from adult trees is described and the significance of departures from random seedling dispersion relative to adults is assessed for each species. Secondly, multi-species patterns are described, and their implications for both seedlings and adults discussed.

In the analyses, adults are defined as trees 100 cm gbh and over in the emergent species of *Shorea*, and trees 80 cm gbh and over in *P. malaanonan* and the canopy species: *Vatica* spp, *H. nervosa* and *S. agamii*. This size limit was smaller than that used by Fox (1972), who defined adults as trees over 5 feet in girth (≈152.5 cm), but was similar to the 3 foot girth limit for seed-parents used by Barnard (1956). The assumption was made that large adults would affect surrounding seedlings, even if they were not the true parents. The estimates of number of adults, based on the analyses of seedling aggregation patterns obtained from Ripley's second-order analysis, $\hat{K}(t)$, in Chapter 7, were similar to the observed number of adults as defined by the girth limits above. Analyses were done for Plot 1 only, as the seedling study area of Plot 2 was too small (0.48 ha) and contained too few adult trees to allow the relative dispersion of seedlings and adults to be quantified.

Edge corrections

The tests of spatial pattern used (Chapter 7) either employed adjustments for edge effects (*eg.* the corrected version of Clark & Evans test and Ripley's $\hat{K}(t)$), or used simulation methods in which the edge effects are the same for the simulated and observed data sets (refined nearest neighbour analysis, $G(w)$).

When considering seedling-to-adult distances, one obvious correction to make is to exclude those seedlings which are nearer to the edge of the plot than to their nearest adult. But this means discarding a non-trivial part of the data, and in effect means deciding arbitrarily for those seedlings that the nearest adult lies outside the plot - it may for some, but not all. For the analyses of seedling numbers and density in relation to distance from adult trees, the decision was therefore made to include

all seedlings in the calculations.

8.3.2 Methods

8.3.2.1 Single-species patterns

For each seedling, distance was found to the nearest adult of the same species. To quantify the changes in seedling numbers with increasing distance from adults, seedlings were tallied in 5 m distance classes (annular rings) up to 30 m from conspecific adults. Distances greater than 30 m were pooled. No edge correction was made, and all seedlings in a species were included. This provides information on the numbers of seedlings at increasing distance from adults, but not on changes in density with distance. Because of the increasing area of consecutive annular rings, the region of highest seedling density will not necessarily coincide with peak numbers (Becker *et al.* 1985). Both seedling density and distance from a large adult may be important in mortality regimes (Augspurger 1983b, 1984a, Clark & Clark 1984, Connell *et al.* 1984, Becker *et al.* 1985).

To calculate seedling density it is necessary to know the area of the plot within each distance region from focal adults of each species. This is complicated by the fact that annular rings may lie partly outside the plot boundary, and rings of adjacent trees could overlap. The area of the plot within each distance region (annular ring) was calculated from a grid of points at one metre intervals, giving 20,000 points. The points were tallied in 5 m distance regions for each species of focal adult, and the area found. From area and numbers of seedlings, the density of seedlings in each distance region was calculated (Condit *et al.* 1992). A null (expected) distribution of seedlings in each species was calculated assuming uniform density across the plot, ie. equal density in each distance region. The number expected in each distance region was compared with the observed number using a χ^2 goodness-of-fit test. The ratio of observed to expected numbers of seedlings was calculated for each distance region: a value greater than 1.0 indicates that a higher number of seedlings than expected was present in a distance region, while less than 1.0 indicates fewer seedlings present.

A second method to test the dispersion of seedlings relative to conspecific adults was derived from Hamill & Wright (1986). The method uses the cumulative

distribution function of distances from juveniles to nearest conspecific adult and compares the observed distribution with a null distribution. Hamill & Wright (1986) calculated a null distribution of juveniles from a theoretical random function. They proposed to test the difference between observed and null distributions, using the Kolmogorov-Smirnov test to compare the maximum difference, D, between the distributions with a critical value based on the number of juvenile-to-adult distances involved. However, since the test assumes that D is the maximum of all differences, the value of D depends on the number of times the difference between distributions is tested (ie, on the number of distance classes chosen). If this is not done often enough, the power of the test is diminished (Zar 1984, Hamill & Wright 1986). In addition, Ripley (1981) considers the use of the Kolmogorov-Smirnov test inappropriate because the standard error of the cumulative distribution function varies with distance. Therefore I used simulations to generate the null distributions. The use of simulation methods also overcomes the problem of edge effects since these will be the same for both the null (simulated) and observed populations.

The simulations used the actual number and position of adults in each species. For each species, N randomly positioned seedlings were generated, where N was the observed number of seedlings in the species. The random coordinates were generated using a random number generating function from the NAG library (NAG 1980), called from a FORTRAN programme. Because seedlings were mapped to 0.1 m, the simulated seedlings were also restricted to a 0.1 m grid, giving 1000 x 2000 possible locations in the plot. Distance was found from each simulated seedling to the nearest (conspecific) adult, and the cumulative seedling-to-adult distance distribution found for the simulated data set. For each species, 99 sets of random seedlings were generated. What this does in effect is to sample 99 permutations of the placement of N seedlings in 1000 x 2000 grid positions. Barnard (1963) suggests regarding the statistics from the observed distribution as another simulation, so the probability that it is the rth most extreme of m simulations is r/(m+1). Seedlings were tallied in one metre distance intervals. The maximum distance for consideration in the test was 50 m.

The maximum and minimum values of the cumulative distribution function from the 99 simulations provide a 1% significance envelope. Where the observed distribution curve lies above the 99% confidence envelope at any distance, there are

more seedling-to-adult distances than expected under the random hypothesis, ie, at that distance, seedlings are significantly under-dispersed (clumped) relative to adults. If the observed distribution falls below the envelope, seedlings are over-dispersed relative to adults. At small distances, this would suggest inhibition, providing some evidence for the existence of spacing mechanisms.

Comparison of the simulated and observed distribution curves reveals therefore not only clumping or over-dispersal of seedlings, but also the scale at which the observed distribution departs from randomness. It is possible for seedlings to be clumped relative to adults at one scale, and over-dispersed at another. This could arise if for example seedlings were dispersed in dense seedling shadows around an adult, but effective seed or seedling predation limited recruitment near the adults (the Janzen-Connell effect). The result would be over-dispersal (inhibition) of seedlings relative to the adults at small scales, say 1-10 m, and clumping at larger distances.

The method has been used to test the relative dispersion of juveniles and adults of Colorado Desert shrubs (Howe & Wright 1986, Wright & Howe 1987).

8.3.2.2 Multi-species patterns

Seedlings were assigned to the nearest adult dipterocarp (as defined above) of any species. This divides the plot into the polygons, or 'territories', associated with each tree, ie, the areas, and associated seedlings, which are closer to that tree than to any other tree (Hubbell & Foster 1987). In effect, a Dirichlet tessellation (Diggle 1983), or S-mosaic (Pielou 1977) was constructed. The group of seedlings within the 'territory' of a tree are described as 'beneath' that tree.

Specific identity of nearest adult

From the point of view of the individual seedling, the dispersion pattern will affect the likelihood that the nearest adult is conspecific or heterospecific. If distance-dependent predation (Janzen 1970), or pathogen attack occur (Augspurger 1983b) this likelihood will be an important factor in seedling survival.

For each seedling, the identity of its nearest adult dipterocarp tree (NA) was recorded as either conspecific or heterospecific. The observed number of seedlings in each species with conspecific NA was compared with an expected value, derived from assigning identities of adults at random and according to the observed

proportion of each species. Under this hypothesis, the chance of a seedling's NA being of the same species was therefore equal to the proportion of adults of that species out of the total population of adults. For example, if a quarter of large trees are species A, then there is a 0.25 chance that a seedling of species A will have a conspecific NA. Differences were tested with a χ^2 test of goodness-of-fit. This null hypothesis ignores the effect of the spatial locations of the adult trees and the associated 'territories'. An alternative null hypothesis would have been to calculate the expected frequencies from the area of the plot within the 'territory' of each species of focal adult, ie. the area within which a seedling would have the focal tree as its nearest adult. The joint 'territory' of two trees of the same species sited close together will be smaller than if the trees were more distant. The approach adopted regards the two trees as independent individuals, whereas the alternative approach would reduce their influence. Thus, each large tree had an equal chance of being the NA, regardless of the spatial patterning of the adults.

Species composition of seedlings beneath focal adults

Focusing on the seedling population, the null hypothesis was tested that seedlings were distributed at random beneath adult trees with respect to species composition, ie. that species composition of the seedling population was independent of the identity of the adult. Density and frequency of conspecific and heterospecific seedlings were compared at increasing distances from focal adult trees of different species.

8.3.3. Results

8.3.3.1 Single-species patterns

Distribution of seedling to nearest adult distances

Frequency distributions of edge-corrected seedling-to-adult distances are shown in Figure 8.2, in which seedlings closer to the plot boundary than to their nearest conspecific adult were excluded. In most species, the distributions were positively skewed: there was an excess of small NA distances. Modal distance class in most species was 10-12 m.

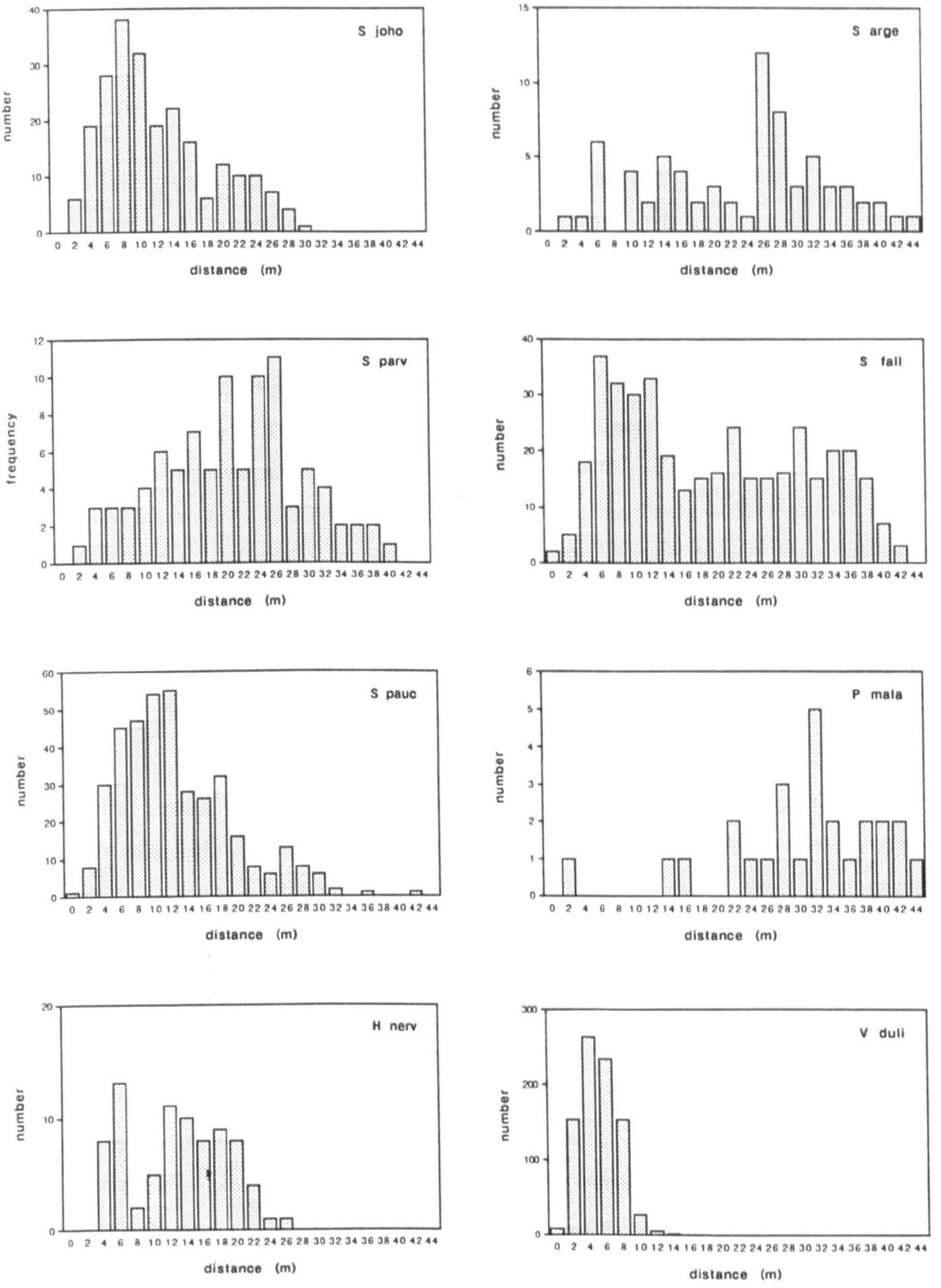


Figure 8.2 Frequency distributions of seedling to nearest conspecific adult distances (edge-corrected) in Plot 1.

Relationship between seedling number, density and distance from nearest adult

Cumulative percentages of seedlings in increasing distance regions from conspecific adults are shown in Figure 8.3. There was great variation between species, ranging from *V. dulitensis*, in which 97% of seedlings were within 10 m of the single conspecific adult, to *P. malaanonan* and *S. agamii* with less than 1% of seedlings within 10 m of conspecific adults. In *P. malaanonan*, less than 2% of seedlings were within 25 m of an adult tree.

The three LRMs had similar patterns: 4 to 6% of seedlings were within 10 m of adults, and 14 to 16% within 20 m. In the other emergent *Shorea* species, the proportions were higher, with 44% seedlings within 20 m in *S. fallax*, and over 68% in *S. johorensis* and *S. pauciflora*. The proportions also differed between the canopy species; in *S. agamii* and *V. sarawakensis*, 13% of seedlings were within 25 m of a conspecific adult, compared to 90% in *H. nervosa*.

The areas of the plot within increasing distance regions of each species of focal adult are given in Appendix 5. Seedling numbers and density within each distance region are given in Table 8.2.

In most species, the distance region with highest seedling density was nearer to the adult than the region with highest seedling frequency. Only one species, *V. dulitensis*, had both highest numbers and frequency in the region nearest the adult trees (<5 m). In one other species, *S. parvifolia*, peak density was within 5 m of conspecific adults, though this represented only seven seedlings. Distributions of seedlings of the two Dark Red Meranti species, *S. fallax* and *S. pauciflora* were similar, with peak density at 5-10 m and peak frequency at 10-15 m. In *S. johorensis*, numbers and density were both highest in the 5 - 10 m distance region. The three LRMs showed differences in trends: *S. argentifolia* seedlings increased monotonically in density with increasing distance from adults up to 20 m distance. Highest density occurred at distances over 30 m. Lowest density of *S. parvifolia* seedlings was at 10 - 15 m distance, and highest at distances over 30 m. In *S. leprosula*, density varied little with distance.

Ratios of observed to expected numbers of seedlings in increasing distance region are plotted in Figure 8.4 for each species. Observed and expected numbers, and results of the χ^2 test for each comparison, are given in Appendix 6. In two species, *S. leprosula* and *V. sarawakensis*, there were no significant departures from expected frequency in any distance region. Because the numbers in each distance

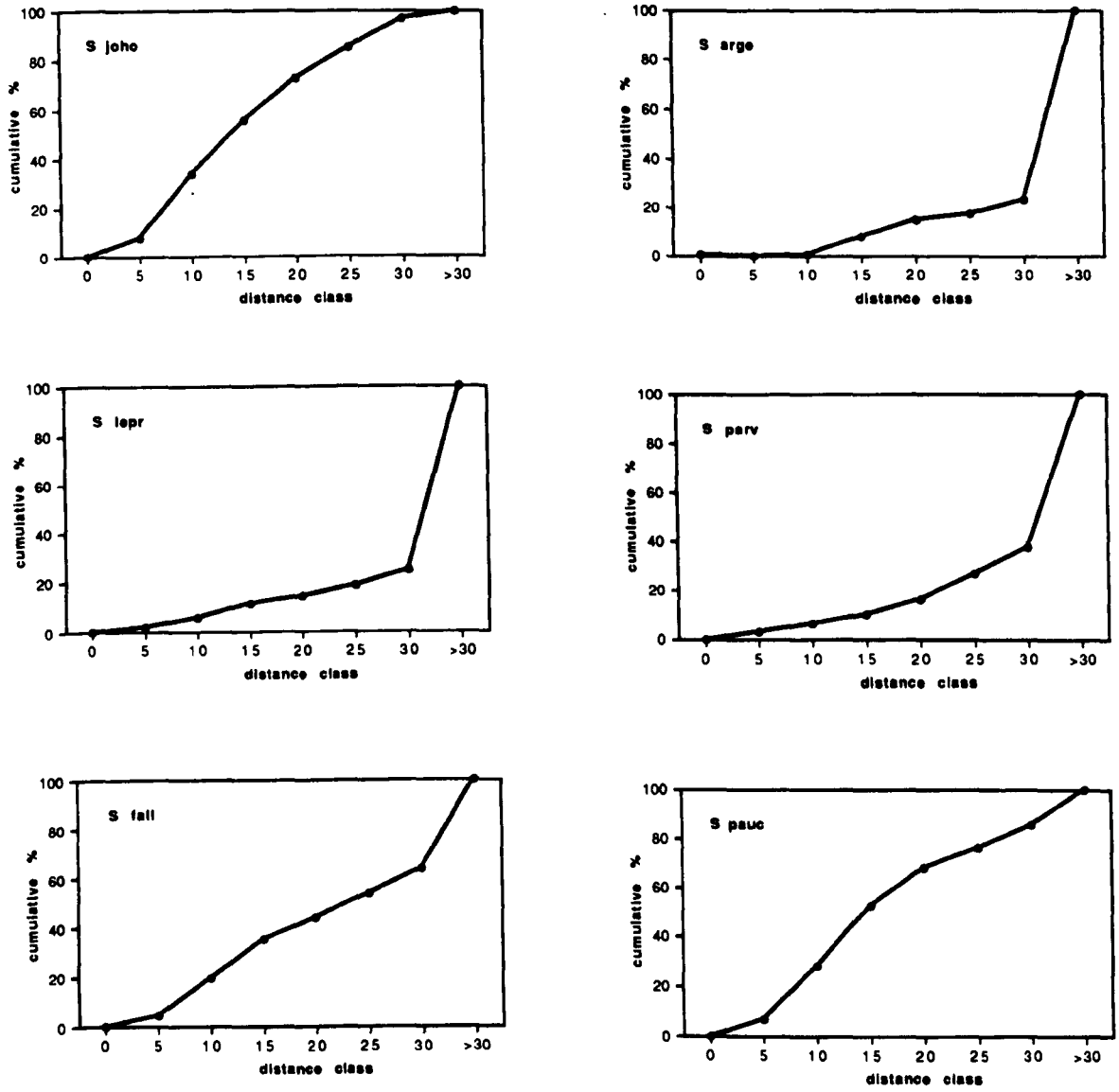


Figure 8.3 Cumulative percentage of conspecific seedlings in 5 m distance regions from focal adults of different species in Plot 1.

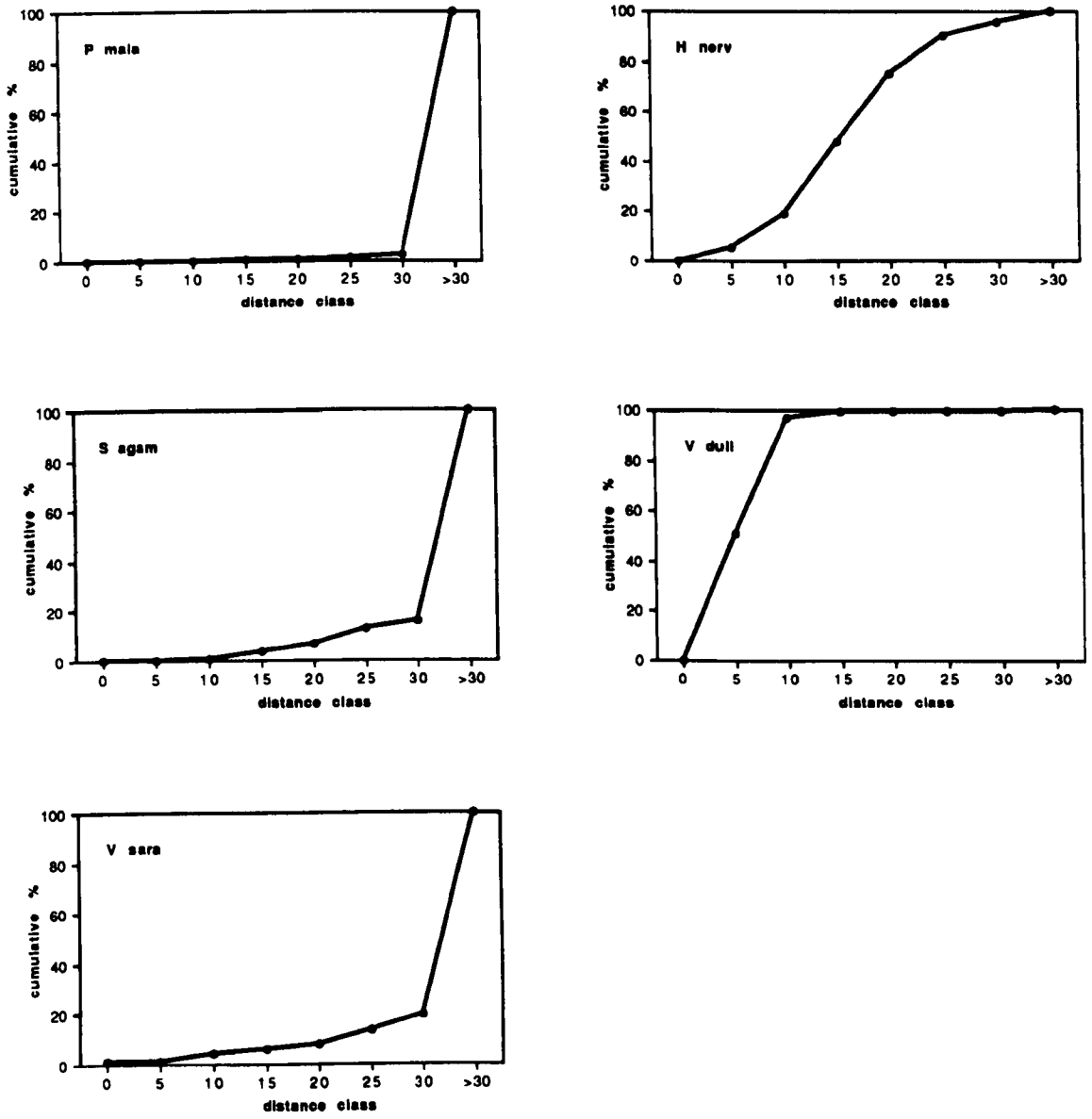


Figure 8.3 (continued) Cumulative percentage of conspecific seedlings in 5 m distance regions from focal adults of different species in Plot 1.

Table 8.2 Numbers (N) and density (D, ha^{-1}) of conspecific seedlings in 5 m distance regions from focal adult trees for different species in Plot 1. The region with the highest number and density within each species is shown in bold. The areas of the plot within each distance region from each species of focal adult tree are given in Appendix 5.

	Distance region (m)													
	> 0 - 5		5 - 10		10 - 15		15 - 20		20 - 25		25 - 30		> 30	
Species	N	D	N	D	N	D	N	D	N	D	N	D	N	D
S joho	25	201.0	88	281.5	73	174.9	56	133.6	42	129.7	38	179.8	11	57.5
S arge	2	45.8	7	65.8	11	87.9	16	114.1	7	49.8	14	106.8	**188**	**143.2**
S lepr	3	82.0	6	61.5	9	81.7	4	35.3	7	56.5	10	75.8	**118**	**85.1**
S parv	7	**248.2**	6	75.9	8	63.8	13	75.5	22	106.5	23	106.3	131	111.7
S fall	27	1163.8	92	**1381.4**	98	1024.6	57	575.8	60	551.0	63	516.0	227	152.9
S pauc	39	821.1	116	948.5	137	**840.0**	87	527.6	44	270.6	50	351.1	81	67.7
P mala	1	33.7	0	0.0	2	20.1	2	19.6	3	26.2	6	57.5	**575**	**391.4**
H nerv	8	509.6	18	380.5	**40**	**578.9**	37	469.5	21	246.5	8	83.8	6	3.7
S agam	0	0.0	1	42.6	5	127.2	5	108.2	10	**191.2**	5	84.5	135	76.2
V duli	**432**	**54000**	**394**	**6694.9**	19	487.2	0	0.0	0	0.0	0	0.0	1	0.6
V sara	1	46.7	3	58.6	2	29.5	2	23.1	5	47.7	6	48.2	**78**	50.5

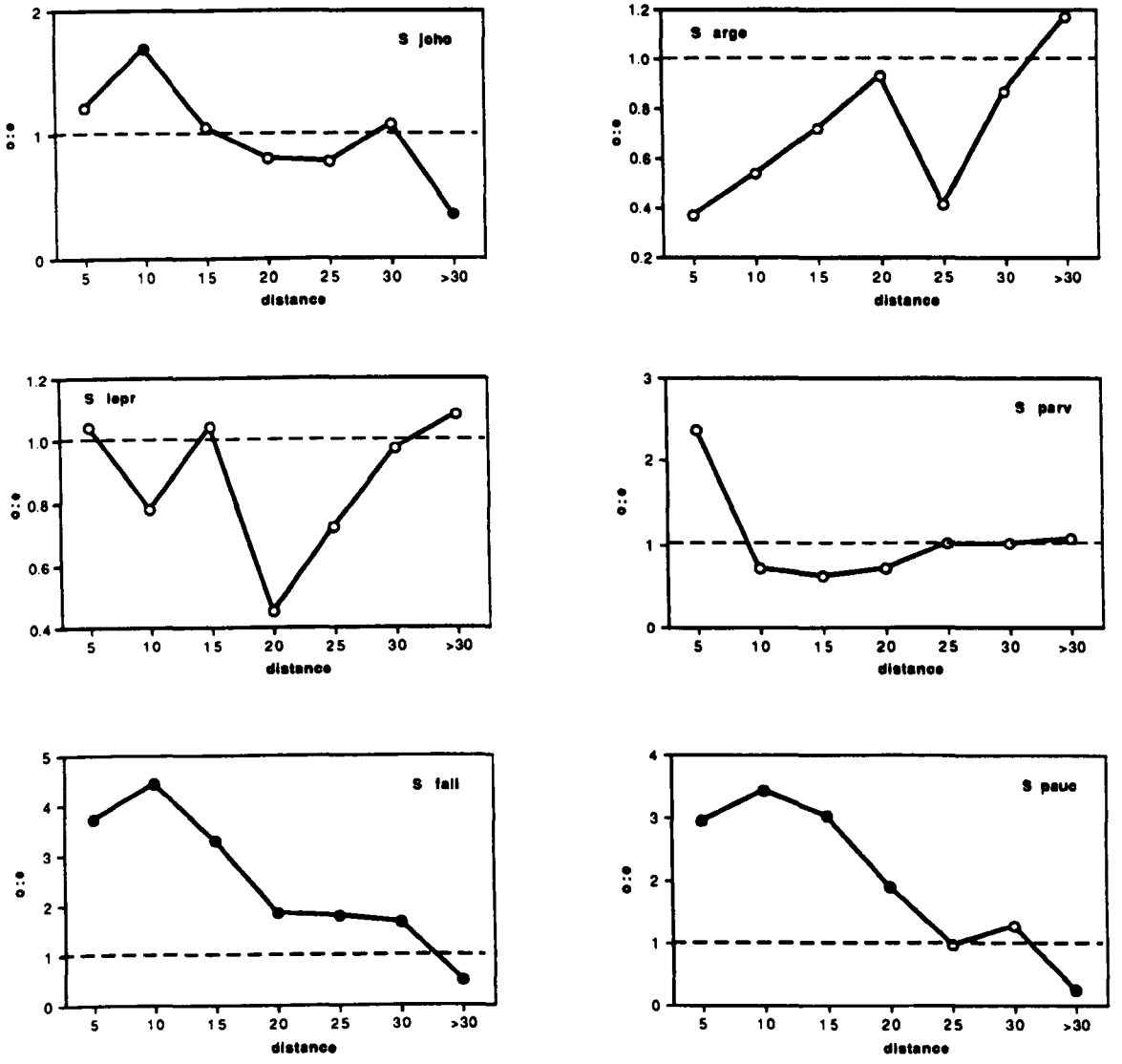


Figure 8.4 Ratio of observed to expected (o:e) numbers of seedlings in 5 m distance regions from conspecific adults in different species in Plot 1. Ratio of 1.0 indicates observed=expected. Filled symbol indicates significant difference between observed and expected (χ^2 test; $P<0.007$, see Appendix 6). Points are plotted at the upper limit of the distance interval, i.e. the point at 10m is for the 5-10 m region.

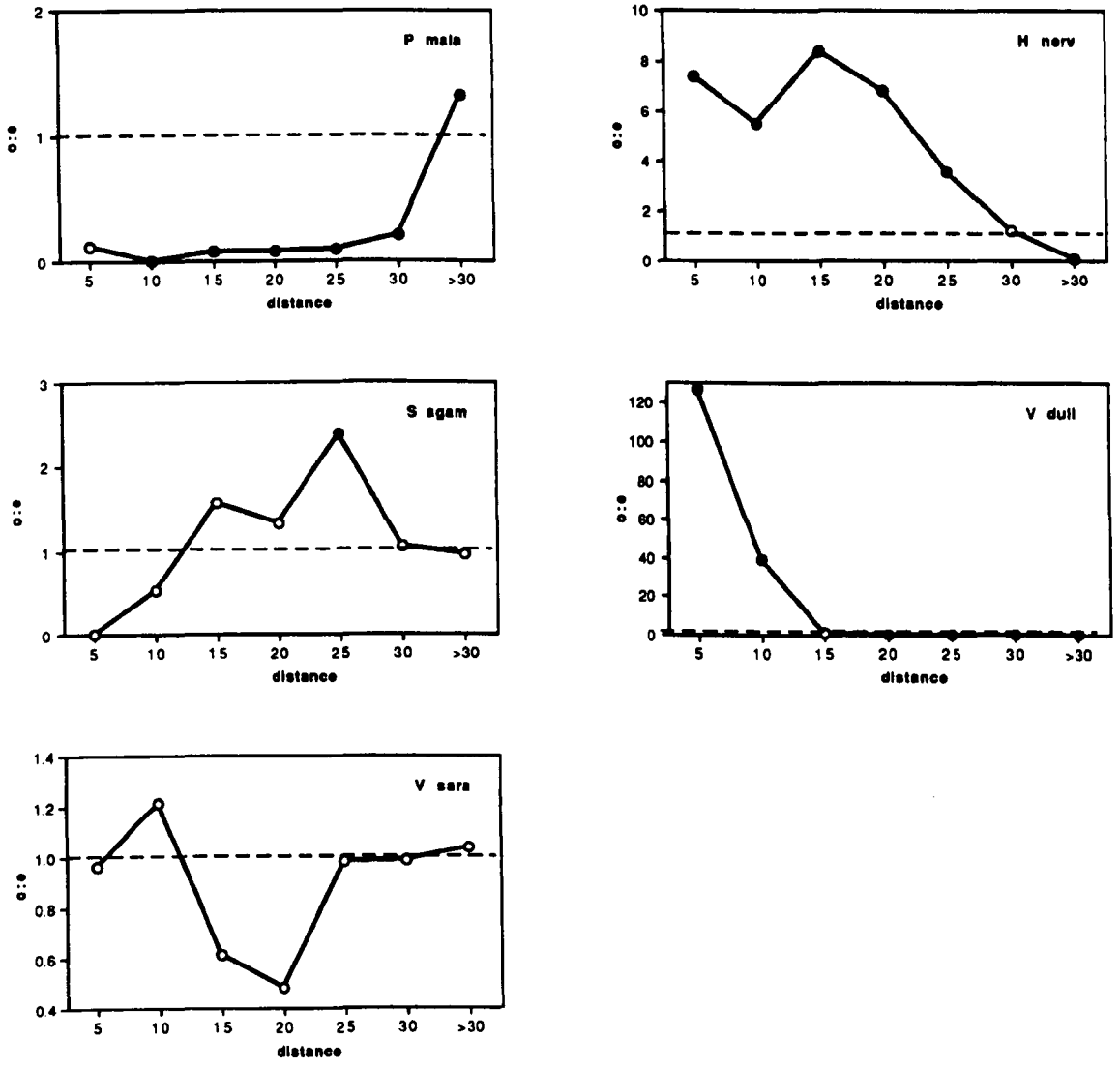


Figure 8.4 (continued) Ratio of observed to expected (o:e) numbers of seedlings in 5 m distance regions from conspecific adults in different species in Plot 1. Ratio of 1.0 indicates observed=expected. Filled symbol indicates significant difference between observed and expected (χ^2 test; P<0.007, see Appendix 6). Points are plotted at the upper limit of the distance interval, i.e. the point at 10m is for the 5-10 m region.

region within species are not independent, a significance level of 0.05/7 (= 0.007) was adopted as a more conservative assessment of significance (corresponding to χ^2=7.24, df=1, obtained by linear interpolation). In *S. fallax* and *P. malaanonan*, seedling numbers were significantly different from expected in every distance region. The contrast between *P. malaanonan* and *V. dulitensis* was again striking.

Cumulative distribution of seedling-to-adult distances

Cumulative distribution functions for seedling-to-adult distances in eleven species are illustrated in Figure 8.5. Results are summarised in Table 8.3. For some configurations of adult placement and numbers of seedlings, not all seedlings were included in the maximum distance limit of 50 m, and the cumulative frequency curve therefore did not reach 1.0.

In three species, *S. leprosula, S. parvifolia* and *V. sarawakensis*, dispersal of seedlings relative to adults could not be distinguished from random at any distance (Figure 8.5). The other species showed either significant clumping or over-dispersal relative to adults at a range of distances. In two species, seedling numbers were significantly (at the 1% level) lower than expected over parts of the distance range: in *P. malaanonan*, there were fewer seedlings than expected between 5 and 50 m from adults, and in *S. argentifolia* the range was 12 - 17 m and 24 - 48 m (Table 8.3). The remaining six species showed significant clumping of seedlings relative to adults at a range of scales. Because of the use of cumulative distribution curves, the effect of an excess of seedlings near adults is carried over to larger distances. In four of the species, significant clumping starts at less than four metres from adult trees, and at 8 m in *S. johorensis* (Table 8.3). In *S. agamii*, seedlings are 'clumped' in the range 38-50 m. This scale is too large for limited seed dispersal to be a cause.

There was no evidence in this test of significant inhibition at the small scale of immediate proximity (5-10 m) of adult trees. However, the fact that significant clumping was not observed immediately around adult trees, ie. at distances of less than 5 m, may be indirect evidence of inhibition, assuming that seed fall was initially highest nearest to the adult.

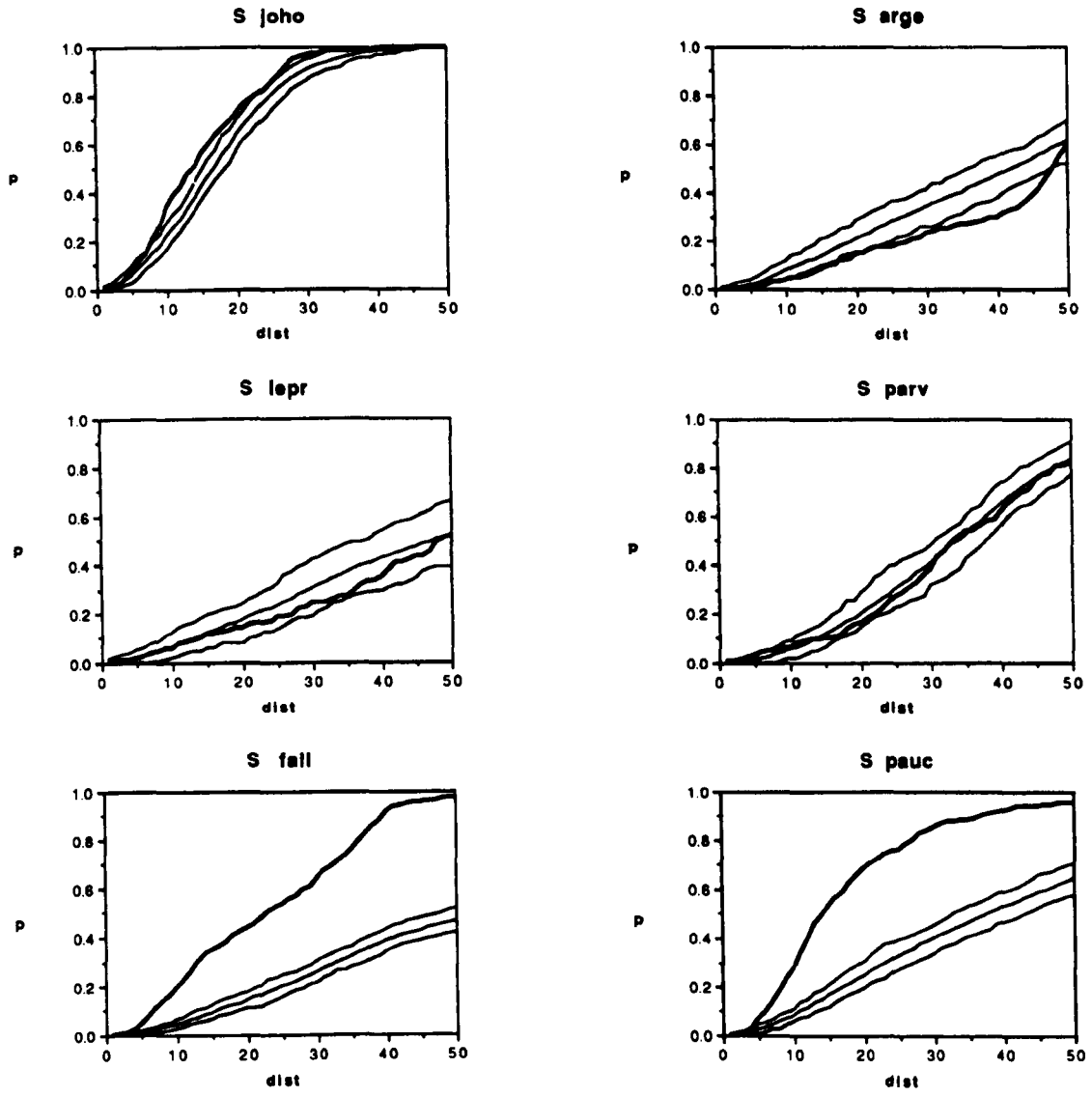


Figure 8.5 Cumulative distribution (p, bold line) of seedling to nearest conspecific adult distances for different species in Plot 1, plotted against distance (m). Mean and 1% significance limits are from 99 simulated data sets.

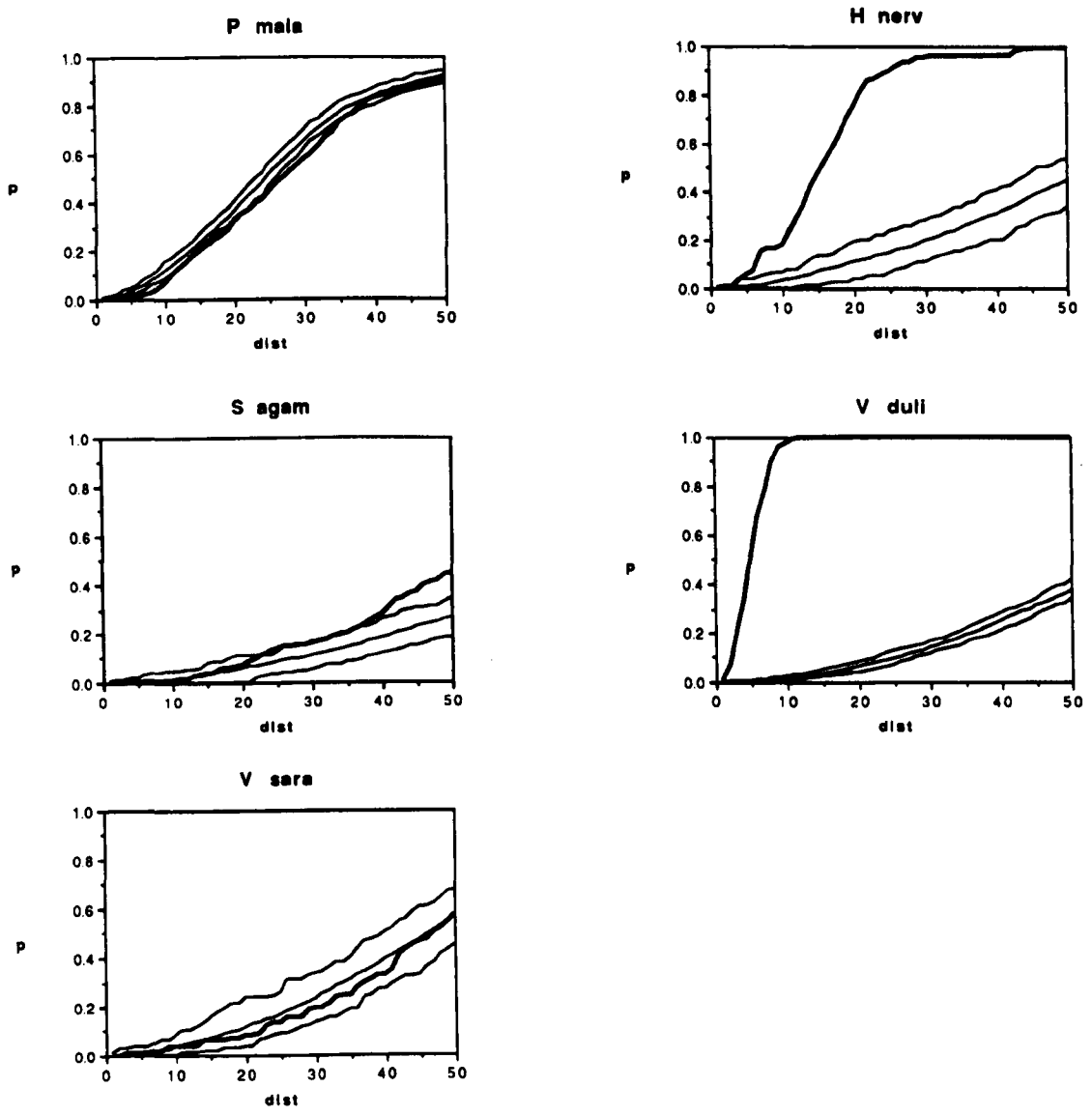


Figure 8.5 (continued) Cumulative distribution (p, bold line) of seedling to nearest conspecific adult distances for different species in Plot 1, plotted against distance (m). Mean and 1% significance limits are from 99 simulated data sets.

Table 8.3 Summary of results of test of seedling and adult relative dispersion. The value d_{max} is the maximum difference between the observed and simulated seedling-to-adult distance distributions. Nature of departure from randomness is given, with the range of distances over which the observed seedling-to-adult distribution differed significantly from simulated distributions (Fig. 8.5).

Species	d_{max}	Nature of difference	Distance of d_{max} (m)	Distance range (metres)
S joho	0.135	clumped	15	8 - 36
S arge	0.177	inhibited	48	12 - 17
S lepr	0.101	N.S.	-	-
S parv	0.045	N.S.	-	-
S fall	0.541	clumped	42	5 - 50
S pauc	0.455	clumped	29	4 - 50
P mala	0.077	inhibited	30	3 - 12; 22 - 35
H nerv	0.768	clumped	29	5 - 50
S agam	0.185	clumped	-	38 - 50
V duli	0.968	clumped	14	2 - 50
V sara	0.068	N.S.	-	-

8.3.3.2 Multi-species patterns

Identity of nearest adult

Results are in Table 8.4. There was huge variation between species in the proportion of seedlings with a conspecific nearest adult, covering the range from less than 1% of *P. malaanonan* seedlings, to 95% in *V. dulitensis*. Frequency of seedlings with conspecific nearest adult differed significantly from expected in all species except *S. parvifolia*. In the other two LRMs, *S. leprosula* and *S. argentifolia*, and in *P. malaanonan*, frequency was significantly lower than expected. In all other species, a seedling was significantly more likely to have a conspecific nearest adult. In *S. johorensis* and *S. pauciflora*, the two most abundant species in terms of basal area of large trees, the proportion of seedlings with conspecific nearest adult was over 50%, compared to between 4% and 7% in the three Light Red Meranti species.

Species composition of seedlings beneath focal adults

The proportions of seedlings of different species beneath eight species of focal adult tree are shown in Figure 8.6. There were large differences between species in the proportion of conspecific seedlings beneath focal adult trees. In three species, *S. fallax*, *S. pauciflora* and *H. nervosa*, conspecific seedlings formed a larger proportion of the seedling population beneath adult trees than any other single species. *S. fallax* formed the highest proportion of seedlings beneath three other species of focal adult: *P. malaanonan*, *S. johorensis* and *S. argentifolia*. *P. malaanonan* was the most abundant species beneath *S. leprosula* and *S. parvifolia* adults, and made up one quarter of the seedlings below *S. pauciflora* adults. In contrast, *S. pauciflora* seedlings formed less than 2% of the seedling population beneath *P. malaanonan* adults. *S. fallax* and *S. pauciflora* seedlings seem to avoid each other's adults. The pattern of overlapping seedling shadows around adults of different species, often patchily-distributed, produced complex patterns of interactions.

Numbers of conspecific and heterospecific seedlings in increasing distance regions from different species of focal adult tree are compared in Table 8.5. Distances up to 20 m are included. Beyond this distance, the area of the plot within the 'territory' or polygon of each adult tree was negligible for most individuals. Numbers of both conspecific and heterospecific seedlings peaked at 5 - 10 m from adults in most species. (Numbers differ from those in Table 8.2 because in Table 8.5 seedlings were assigned to the nearest adult of any species, and not the nearest conspecific

Table 8.4 Numbers and percentage of seedlings in each species whose nearest adult tree was conspecific in Plot 1. Adults were defined as trees ≥80 cm gbh in *H. nervosa* and *Vatica* spp. and ≥100 cm gbh in other species. Observed number was compared with expected (Exp) in each species with a χ^2 goodness-of-fit test (df=1).

Species	Number of adults	Seedlings with conspecific nearest adult			χ^2	P	Fewer/more than expected
		Number	%	Exp.			
S joho	17	161	48.3	109	24.97	***	more
S arge	6	9	3.7	28	13.13	***	fewer
S lepr	5	10	6.4	15	1.72	N.S.	-
S parv	4	13	6.2	16	0.59	N.S.	-
S fall	3	121	19.4	36	200.69	***	more
S pauc	6	292	52.7	64	813.78	***	more
P mala	4	1	0.2	45	43.33	***	fewer
H nerv	2	77	55.0	5	968.37	***	more
S agam	1	3	1.9	3	0.003	N.S.	-
V duli	1	806	95.4	16	38381.85	***	more
V sara	3	4	4.1	6	0.46	N.S.	-

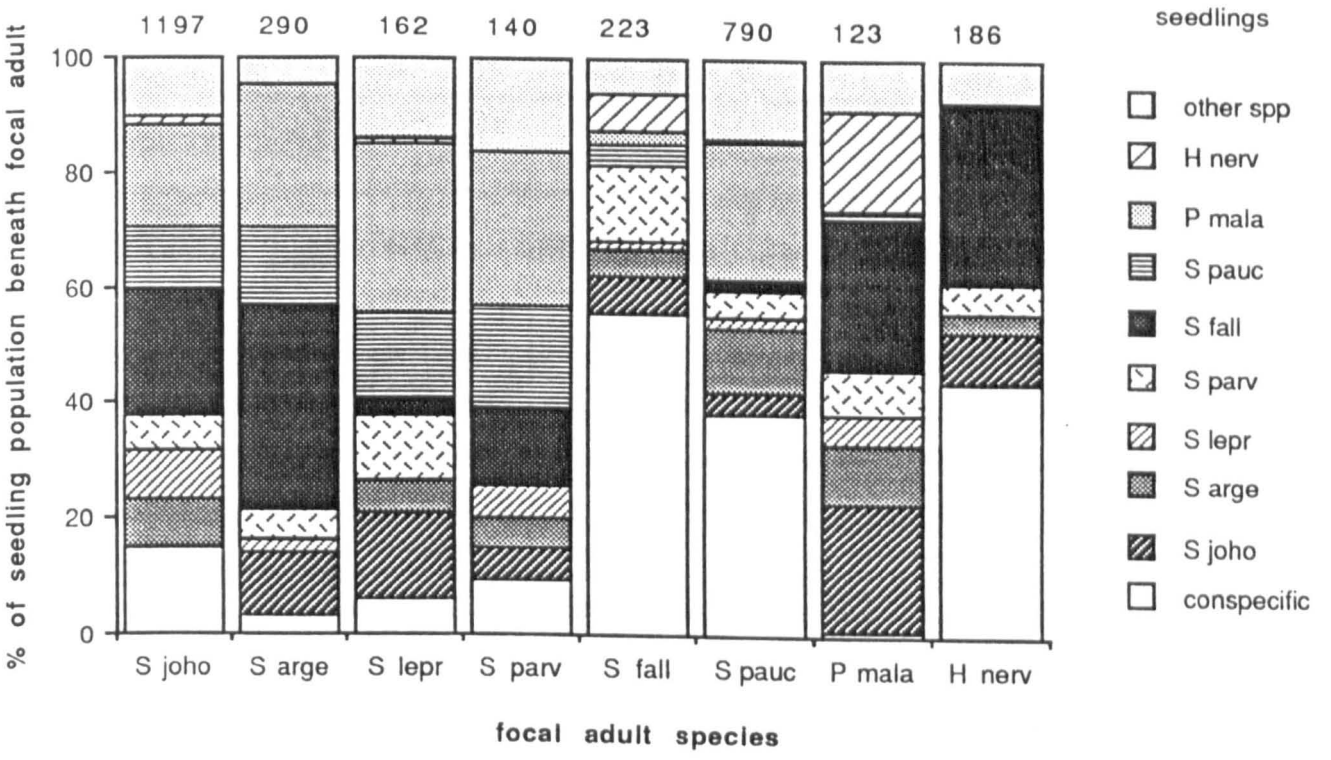


Figure 8.6 Comparison of species composition of seedlings, expressed as % of total seedlings, beneath (and within 20 m) different species of focal adult tree in Plot 1. The total number of seedlings beneath each species of focal adult species is given above each column.

Table 8.5 Comparison of numbers of conspecific (C) and heterospecific (H) seedlings in 5 m distance regions from different species of focal adult trees in Plot 1, with (in brackets) the percentage of conspecific seedlings in each distance region. Total density within the plot is given (expressed as number per 10x10 m quadrat). Highest numbers of conspecific and heterospecific seedlings for each focal adult species are shown in bold.

	Distance region (m)							
	< 5	5 - 10	10 - 15	15 - 20	Total number		Total density per 10x10 m	
Species	C H	C H	C H	C H	C H		C H	
S joho	24 169 (12.4)	**79 356** (18.2)	44 281 (13.5)	12 115 (8.8)	161 943 (14.6)		2.6	15.1
S arge	1 42 (2.3)	5 **117** (4.1)	2 55 (3.5)	0 24 (0.0)	9 263 (3.31)		0.4	13.2
S lepr	3 20 (13.0)	1 **51** (2.0)	**6** 32 (15.8)	0 9 (0.0)	10 112 (8.2)		0.7	8.4
S parv	**6** 17 (20.7)	2 **39** (4.9)	2 35 (5.4)	3 27 (10.0)	13 120 (9.8)		0.9	8.3
S fall	25 7 (78.1)	**70 43** (61.9)	18 18 (50.0)	8 14 (36.4)	121 82 (59.6)		10.8	7.3
S pauc	39 53 (42.4)	**110 194** (36.2)	98 152 (39.2)	39 72 (35.1)	292 481 (37.8)		8.9	14.7
P mala	1 29 (3.3)	0 **47** (0.0)	0 36 (0.0)	0 9 (0.0)	1 122 (0.8)		0.1	10.4
H nerv	8 20 (28.6)	17 55 (23.6)	**33** 62 (34.7)	19 **69** (21.6)	77 221 (25.8)		5.2	14.8
S agam	0 0 -	**2** 2 (50.0)	0 **6** (0.0)	1 **6** (14.3)	3 14 (17.6)		1.6	7.7
V duli	**432** 8 (98.2)	370 **27** (93.2)	4 25 (13.8)	0 8 (0.0)	806 68 (92.2)		164.5	13.9
V sara	1 11 (8.3)	**2** 31 (6.4)	1 28 (3.6)	0 9 (0.0)	4 79 (4.8)		0.3	6.5

adult). Peak conspecific density occurred at less than 5 m from adults in four species, and at 5-10 m in five species

In *S. fallax*, *S. pauciflora* and *H. nervosa* conspecific seedlings formed over 20% of the total dipterocarp seedling population in all distance regions up to 20 m. In most other species the proportion of conspecific seedlings declined with distance from adults. In two species, *S. fallax* and *V. dulitensis*, density of conspecific seedlings was higher than density of all other species combined. Total dipterocarp seedling density beneath adult trees varied by a factor of 3.4, if *V. dulitensis* is excluded. Density was highest beneath *S. pauciflora* and lowest beneath *V. sarawakensis*.

8.4 CHANGES IN RELATIVE DISPERSION OF SEEDLINGS AND TREES

Changes in the dispersion patterns of seedlings relative to adults may provide more direct evidence for the existence of spacing mechanisms. Do the observed seedling patterns change over time? If there is a shift in seedling-to-adult distance, what is the direction? An increase in mean seedling-to-adult distance over time may support the Janzen-Connell model (Augspurger 1983a, Clark & Clark 1984). A decrease in seedling-to-adult distance, or enhanced survival closer to adults, may point to an alternative view, that dipterocarps are restricted to areas of suitable habitat.

Ideally, changes in mean seedling-to-adult distance should be monitored in single cohorts from germination (Clark & Clark 1984). Apart from the 1985 cohort of *V. dulitensis* seedlings, the seedling populations in the present study were multiple cohorts of unknown age, but any increase in mean seedling-to-adult distance over the study period will still provide indirect evidence of some form of spacing mechanism. Differential mortality has already been demonstrated in two species in Plot 1 (Chapter 3.6).

Differences in the (static) dispersion patterns of large versus small seedlings provide indirect evidence for the existence of spacing mechanisms (Hubbell 1979, Hubbell & Foster 1987). The Janzen-Connell model predicts that recruitment can only occur beyond a minimum critical distance from the parent tree (Janzen 1970, Connell

1971, Clark & Clark 1984). Large seedlings should therefore be found further from adult trees than small seedlings, i.e. mean seedling-to-adult distances should increase with seedling size.

The existing patterns are the outcome of past dynamic processes, including differential mortality. From growth simulations (Chapter 4.11), the largest saplings (over 5 m tall) were estimated to be at least 11 years old in the fastest growing species, and over 20 yr in other species, so their dispersion patterns will reflect processes operating over a longer period than the present study.

8.4.1 Methods

8.4.1.1 Evidence from static dispersion patterns

To examine the relationship between seedling size and distance from adults, the seedling-to-nearest-adult (NA) distance for each seedling was plotted against its height. Median NA distances were compared for four height classes of seedlings using Kruskal-Wallis non-parametric analysis of variance. Seedlings nearer the plot boundary than to their nearest conspecific adult were excluded from this analysis. Finally, the emphasis was changed from the seedling environment to the consequences of the dispersion patterns of seedlings for the focal tree, and, by extension, species and population dynamics. A species with a higher proportion of conspecific seedlings beneath it will increase the chance of self-replacement. Does this proportion change with increasing size of offspring?

Seedlings were assigned to their nearest large dipterocarp tree of any species, as before (Chapter 8.3.2.2). No edge correction was made; all seedlings and large trees were included. Proportions of two size classes of seedlings, (≤250 cm and >250 cm tall), and small trees (10.0-19.9 cm gbh) were compared beneath conspecific adult trees. Significance was tested by comparing the observed number of conspecifics in a size class with an expected value, calculated on the assumption that the species composition of seedlings or trees beneath each focal adult species was the same as the overall species composition in the whole plot.

8.4.1.2 Evidence from changes in dispersion patterns

To examine changes in relative dispersion over time, mean seedling-to-adult distance within each species was compared at the first and the final enumeration. Significance was tested using simulation methods as follows. From the total observed seedling population in each species, N survivors were chosen at random, where N was the observed number alive at the final enumeration in that species. Mean NA distance was found for the set of survivors, using the actual coordinates of seedlings and adults. This was repeated 99 times, and the distribution of mean NA distances compared with the observed mean NA distance at the final enumeration. The number of times the observed mean NA distance was equal to or greater than a simulated value was recorded. An edge correction was done in this test because the random death of a seedling a long distance, eg. over 50 m, from an adult tree is not likely to be attributable to an effect of the adult, but its death would have a large effect on the mean NA distance of survivors. Under the random model, each seedling had an equal chance of survival, but only those close to an adult tree were included in the calculation of the test value (mean NA distance), because the intention was to focus on processes in the immediate vicinity of the adult trees. In the simulations therefore, the edge correction was done after survivors had been picked, but before mean NA distance was calculated.

If the observed mean NA distance is larger than the mean from each of the 99 simulations, random mortality can be rejected at the 1% level and there is significant repulsion of seedlings relative to adults. Alternatively, if the observed mean NA is less than all the simulation values, seedlings are significantly attracted to adults over time.

8.4.2 Results

8.4.2.1 Variation in NA distance with size: evidence from static dispersion patterns

The relationship between seedling height and NA distance is illustrated in Figure 8.7. In general, large seedlings were not found close to conspecific adults, whereas small seedlings occurred at a wider range of distances from the adults. On the scatterplots for most species, a line can be drawn representing an increasing

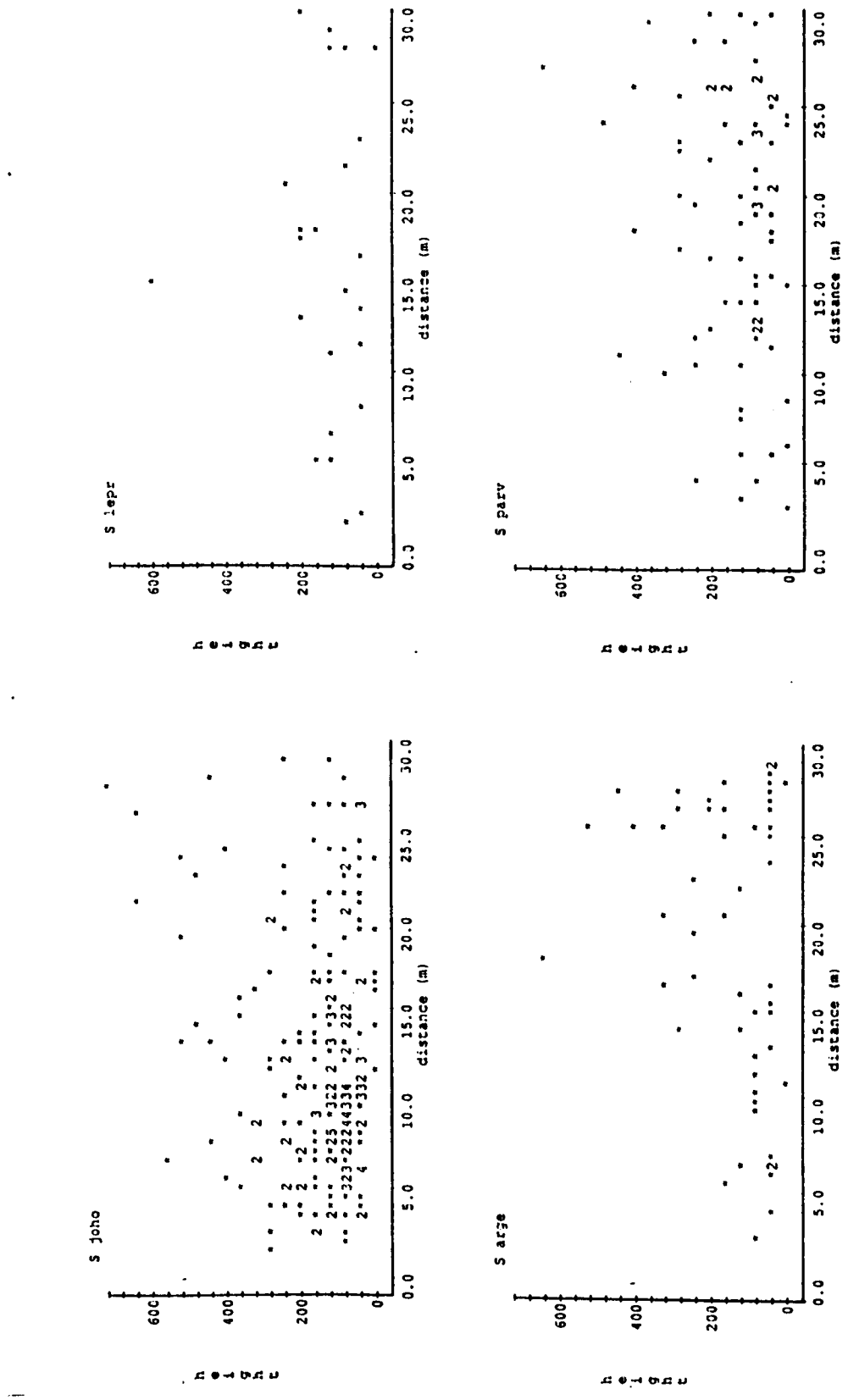


Figure 8.7 Relationship between distance (m) to nearest conspecific adult tree and seedling height (cm) in different species in Plot 1. Numbers in the graphs give the number of seedlings sharing the same values.

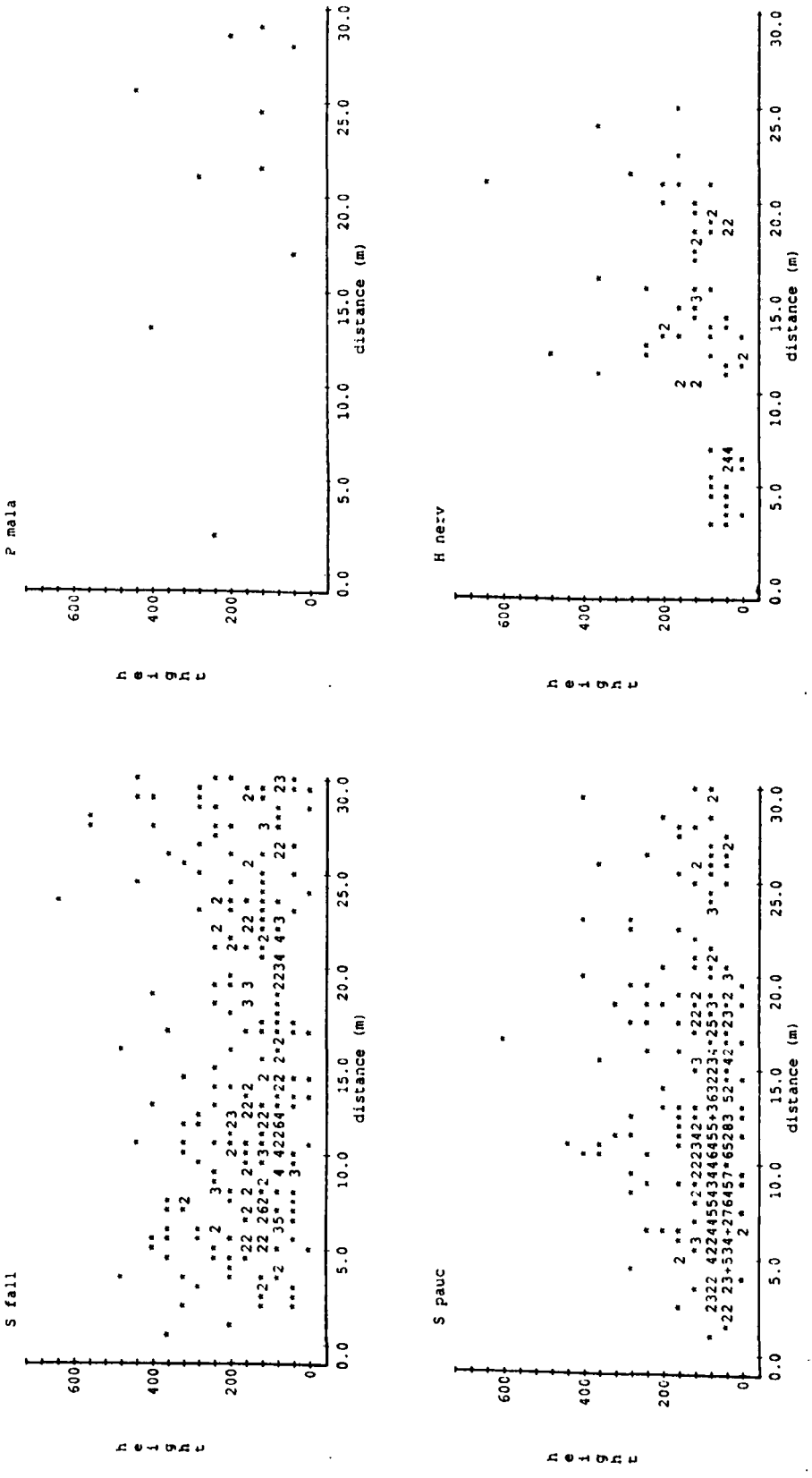


Figure 8.7 (continued) Relationship between distance (m) to nearest conspecific adult tree and seedling height (cm) in different species in Plot 1. Numbers in the graphs give the number of seedlings sharing the same values.

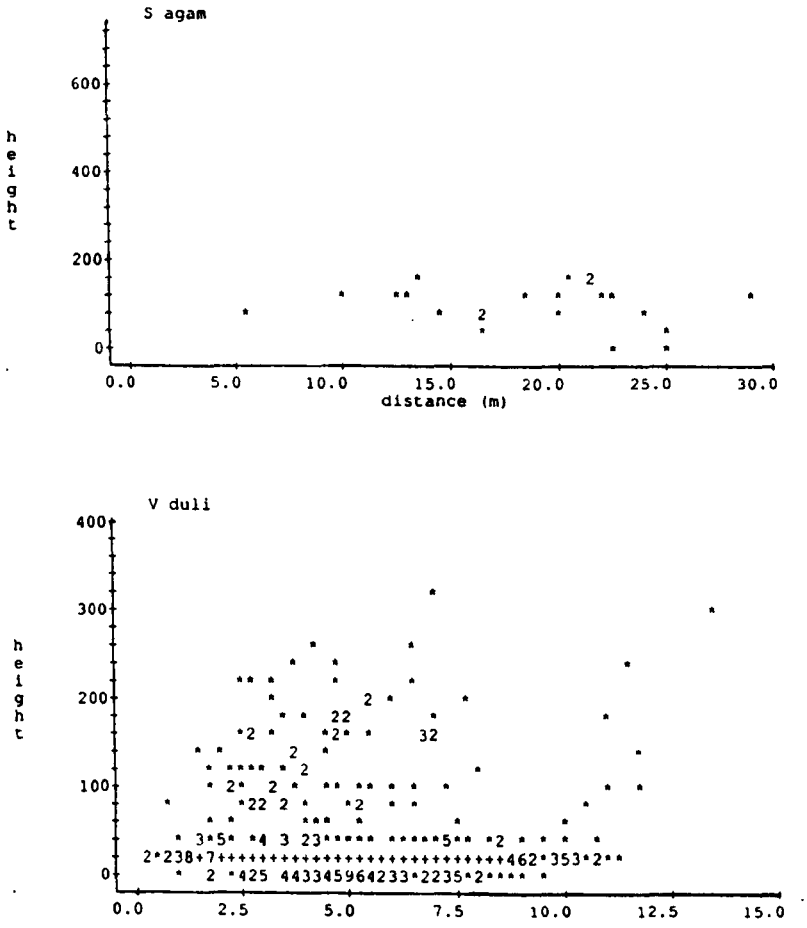


Figure 8.7 (continued) Relationship between distance (m) to nearest conspecific adult tree and seedling height (cm) in different species in Plot 1. Numbers in the graphs give the number of seedlings sharing the same values.

degree of repulsion (i.e. fewer seedlings than expected) with increasing seedling size, such that the great majority of seedlings lie below the line. Median NA distances in four height classes in different species are given in Table 8.6, together with the results of the Kruskal-Wallis tests comparing median NA distances between height classes. There were significant differences in mean NA distance with size in two species, *S. pauciflora* and *H. nervosa*. In both species, the largest seedlings were further from adult trees and the smallest seedlings closest. In *H. nervosa*, seedlings over 2 m tall were twice as far from the adult as seedlings ≤50 cm tall.

In Figure 8.8, height distributions are compared for seedlings growing beneath conspecific versus heterospecific adult trees. Seedlings in the six emergent *Shorea* species growing within 10 m of their nearest adult tree are included. The two distributions were significantly different (χ^2 = 26.65, df=4 [the two largest height classes were pooled], P<0.01). For seedlings growing beneath a conspecific adult, proportions of seedlings in the smallest three height classes were higher than for seedlings beneath heterospecific adults. For the three larger height classes, the situation was reversed: a higher proportion of seedlings below heterospecific adults were in the larger size classes. Double the percentage of seedlings beneath conspecific adults versus heterospecific adults was over 3 m tall (5.7% of seedlings beneath conspecific adults compared to 11.7% below heterospecific adults). This provides further evidence of a shift in height distribution for seedlings below conspecific adult trees.

Proportions of small and large seedlings beneath conspecific trees

The proportion of conspecific seedlings up to than 250 cm tall beneath adult trees was significantly higher than expected from plot proportions in five species, lower than expected in one species (*P. malaanonan*), and as expected in two species (Table 8.7). Expected values were too low for significance to be tested in two species (<1, Zar 1984). There were fewer sapling over 250 cm tall, and in three species the expected value was less than one. Numbers of large conspecific saplings beneath adult trees were significantly higher than expected in two species, *S. pauciflora* and *H. nervosa*. In these two species, χ^2 values were lower than for small seedlings (Table 8.7). The numbers of trees were even lower, and expected values were less than one in all but two species. In these two species, *S. pauciflora* and *S. fallax*, numbers below conspecific adults were no different from expected.

Table 8.6 Comparison of median distance (edge-corrected) from seedling to nearest conspecific adult in four height classes in different species in Plot 1, and results of Kruskal-Wallis test.

Species	Median seedling-to-conspecific adult distance (m)				P
	> 50 cm	51 - 100 cm	101 - 200cm	> 200 cm	
S joho	10.9	10.3	10.5	11.8	N.S.
S arge	27.8	23.7	25.8	25.6	N.S.
S lepr	15.6	21.7	17.8	18.1	N.S.
S parv	19.7	19.5	26.0	20.0	N.S.
S fall	13.1	16.5	17.1	22.2	N.S.
S pauc	10.6	12.0	12.4	16.7	***
P mala	22.4	34.6	33.6	25.7	N.S.
H nerv	6.6	13.0	15.2	15.4	***
S agam	33.1	24.2	44.4	30.5	N.S.
V duli	4.8	3.9	4.6	5.4	N.S.

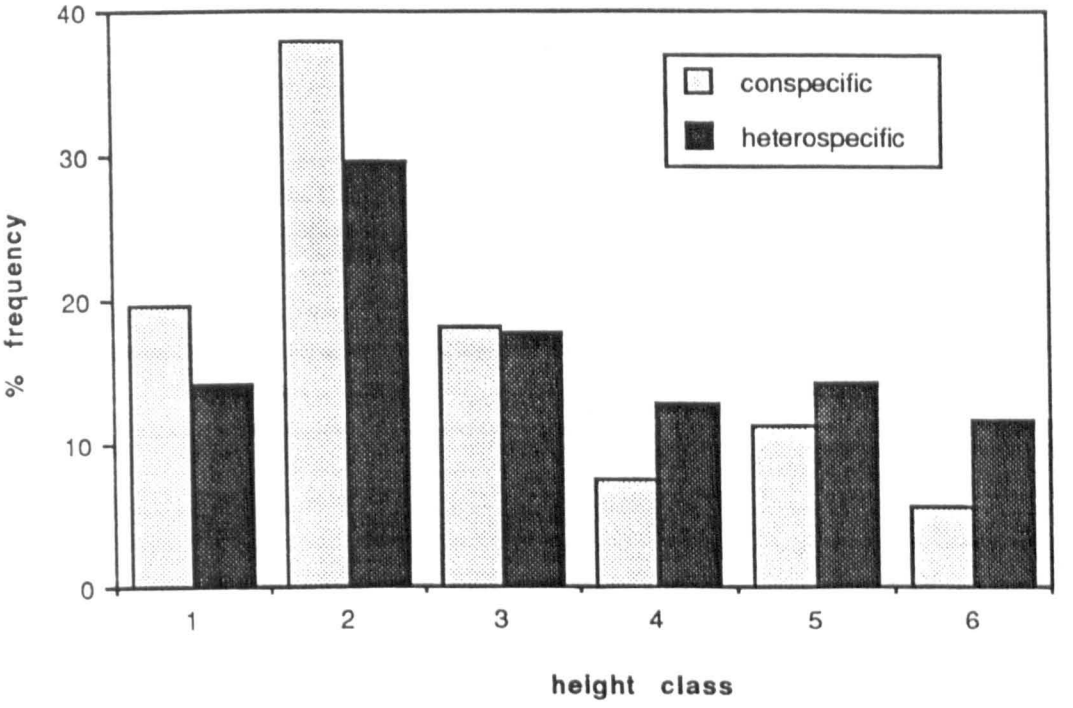


Figure 8.8 Comparison of height distributions (% frequency) of conspecific and heterospecific seedlings growing beneath (and within 10 m) different species of focal adult tree for the six emergent *Shorea* species in Plot 1. Height classes 1 to 4 are in 50 cm intervals; class 5, 201-300 cm; class 6, >300 cm. The two distributions are significantly different (χ^2=26.65, df=4, P<0.001 [the two largest height classes were pooled).

Table 8.7 Comparison of numbers of conspecifics in three size classes beneath different species of focal adult tree in Plot 1. See text for details.

(a) seedlings ≤ 250 cm tall

Focal tree species	Total numbers of seedlings: all spp. beneath focal adult	Total numbers of seedlings: of focal sp. in plot	Numbers of conspecifics Observed	Numbers of conspecifics Expected	χ^2
S joho	1040	287	157	82.8	66.56
S arge	258	217	9	15.5	2.74
S lepr	140	125	9	4.9	3.54
S parv	125	180	13	6.2	7.32
S fall	172	492	103	23.5	269.54
S pauc	739	513	288	105.1	318.08
P mala	98	555	1	15.1	13.15
H nerv	149	119	71	4.9	891.68
S agam	13	148	3	0.5	-
V duli	869	846	803	203.9	1760.60
V sara	3	89	1	0.07	-
Total	3606	3606			

(b) seedlings > 250 cm tall

S joho	157	46	21	18.5	0.35
S arge	32	28	0	2.3	2.29
S lepr	16	32	1	1.3	1.31
S parv	15	30	0	1.2	1.15
S fall	51	132	21	17.2	0.83
S pauc	51	41	13	5.3	10.95
P mala	25	34	0	2.2	2.17
H nerv	37	19	11	1.8	47.10
S agam	1	13	0	0.03	-
V duli	5	5	3	0.06	-
V sara	1	8	0	0.02	-
Total	391	391			

(c) trees 10 - 19.9 cm gbh

species	Total numbers of trees: all spp. beneath focal adult	Total numbers of trees: of focal sp. in plot	Numbers of conspecifics Observed	Numbers of conspecifics Expected	χ^2
S joho	90	18	6	8.7	0.84
S arge	8	10	0	0.4	-
S lepr	7	11	1	0.4	-
S parv	8	13	0	0.6	-
S fall	17	82	10	7.5	0.84
S pauc	24	23	6	3.0	3.10
P mala	11	12	0	0.7	-
H nerv	10	4	2	0.2	-
S agam	1	6	0	-	-
V duli	10	1	0	-	-
V sara	1	3	0	-	-
Total	186	186			

The percentage of conspecific offspring in the three size classes beneath conspecific adult trees are summarised in Table 8.8. With increasing offspring size, there was a reduction in the percentage of conspecifics in eight out of ten species. However, this is also a function of low numbers of larger individuals and small plot area beneath some focal adult species, and in most species the numbers of conspecific offspring beneath adult trees was not different from expected. In *V. dulitensis*, for example, the contrast between small seedlings and trees was great: 95% of seedlings beneath the single adult were conspecific, but there were no conspecific trees. It is likely that the single parent tree reached reproductive maturity only recently, and there has not been time for its offspring to reach tree size.

8.4.2.2 Variation in NA distance over time: evidence from changes in dispersion patterns.

In one species, *S. pauciflora*, observed mean NA distance at the final enumeration was greater than any of the mean NA distances calculated after 99 simulations of random mortality (Table 8.9). In other words, differential mortality resulted in an increase in mean NA distance significant at the 1% level. Mean distance increased from 12.6 m to 13.1 m. In *S. leprosula*, the observed mean NA distance was greater than all but one of the simulated values, ie. significant at the 2% level. Mean seedling-to-adult distance increased from 17.0 m to 18.3 m. In the 1985 cohort of *V. dulitensis*, mean seedling-to-adult distance was greater at the end of the enumeration period, and exceeded only two of the simulated values, indicating a significant decrease in mean seedling-to-adult distance over time. In this species, mortality was higher further from the adult tree. In all other species, mortality was not distinguishable from random with respect to distance from conspecific adults by this test.

Table 8.8 Proportions of seedlings under and over 250 cm tall, and trees 10-19.9 cm gbh beneath different species of focal adult tree in Plot 1. See text for details.

Species	% of conspecifics beneath focal adults			
	all seedlings	seedlings ≤ 250cm	seedlings > 250cm	trees 10 - 19.9 cm gbh
S joho	14.9	15.1	13.1	6.7
S arge	3.1	3.5	0.0	0.0
S lepr	6.2	6.4	6.2	14.3
S parv	9.3	10.4	0.0	0.0
S fall	55.6	59.0	41.2	58.8
S pauc	38.1	39.0	25.5	25.0
P mala	0.8	1.0	0.0	0.0
H nerv	44.1	47.6	29.7	20.0
V duli	92.2	92.4	60.0	0.0

Table 8.9 Comparison of mean seedling-to-nearest-conspecific adult distance (metres, edge-corrected) in different species at start (d_0) and end (d_{final}) of enumeration period in Plot 1, and results of simulations of random mortality.

Species	d_0	d_{final}	N_0	N_{final}	number of times d_{final} > simulated d_{final}
S joho	12.2	12.3	236	185	73
S arge	23.0	23.7	71	57	73
S lepr	17.0	18.3	26	20	98
S parv	20.6	20.9	92	78	83
S fall	19.3	19.2	394	369	33
S pauc	12.6	13.1	387	335	99
V dul1‡	4.89	4.82	514	465	15
V dul2‡	5.21	5.12	333	134	2

‡ V dul1 - seedlings older than 1985 cohort
V dul2 - seedlings of 1985 cohort

8.5 DISCUSSION

Seed dispersal and consequences

In a series of trials with model fruits, Augspurger & Franson (1987) found that variation in wing-loading influences not just distance but evenness of dispersion: low wing loading results in both further dispersal and more even distribution of seeds. They found that the model fruits with the lowest wing loading had the greatest median dispersal distances, and were distributed the most evenly over the widest area. A change in wing-loading produced greater change in the evenness of distribution than in the distance dispersed. In the present study the species which were not aggregated with respect to adults were also well-distributed throughout the plot. These were the Light Red Merantis and *P. malaanonan*. (Distances from seedling-to-adult in the plot were difficult to quantify accurately because seedlings with long seedling-to-adult distances were likely to be closer to the edge of the plot than to their nearest adult within the plot, and their nearest adult could have been outside the study area.)

Light Red Merantis tended to have relatively low Wing-Loading Index (WLI), random or weakly aggregated seedling patterns, and numbers of seedlings in vicinity of adults were not different from expected. The Dark Red Merantis and *H. nervosa* had higher WLI, and seedlings were strongly aggregated with respect to adults. *S. fallax* had a higher WLI than all other *Shorea* species (0.41, compared with a range of 0.20 to 0.24 in the other species), and had the most clumped distribution pattern of the *Shoreas*, and the most aggregated relative to adult trees. However, in *S. pauciflora* seedling dispersion patterns very similar to *S. fallax*, but WLI was similar to the other *Shoreas*. *H. nervosa* had similar WLI to the more evenly distributed *Shorea* spp., but had strongly aggregated seedlings: it is likely that the smaller stature of the adult trees (within the canopy) limits fruit dispersal. Poore (1968), in Jengka Forest Reserve, noted that the "correlation between pattern and means of dispersal is not reliable", and observed that *S. leprosula* and *S. macroptera* fruits were the same size, but *S. leprosula* was almost randomly dispersed, while *S. macroptera* was clumped. These species (the three LRMs, and to a lesser extent, *S. johorensis*) each had low WLI, suggesting that seeds may initially be better dispersed than in other species. *P. malaanonan* had the largest wing area, though not the lowest WLI, and has one of the

least clumped seedling dispersion patterns, as well as the most repelled pattern of seedlings relative to adults (i.e. there were significantly fewer seedlings than expected close to adult trees). *S. parvifolia* had the lowest WLI and was dispersed randomly with respect to adult trees, and had only marginally aggregated seedlings.

Vatica species have virtually wingless nuts (Ashton 1982), but there was a striking contrast between spatial patterns of the two species present, *V. sarawakensis* and *V. dulitensis*. *V. sarawakensis* had the largest nut of all species in study area, yet had the most randomly distributed seedlings, and seedlings which were over-dispersed relative to adults. *V. dulitensis* has smaller nuts, and had a very strongly clumped seedling pattern. In a third species (not present in the seedling study areas), *V. umbonata*, large numbers of germinating fruit were observed immediately beneath the parent tree in July 1988 1 km west of the Field Station. To account for the random dispersion observed in *V. sarawakensis* despite the large fruit, it seems likely that this species has some means of active secondary dispersal. Rats are known to scatter-hoard the larger dipterocarp fruits, but probably do not disperse them far (Ashton 1988b). The large seeds of *V. sarawakensis* (ca. 2.5 cm diameter) may be particularly attractive to rodents.

Spatial aspects of recruitment

In a test of the Janzen-Connell model at the community level in the 50 ha plot on BCI, Condit *et al.* (1992) calculated the recruitment probabilities of each species relative to all other species. The spatial dynamics of recruitment (individuals entering the 1 cm dbh class) over a three year period was studied in 80 species of trees and shrubs. From the patterns exhibited by recruitment, they identified four 'recruitment syndromes': 'attracted' - in which there was a significant excess of recruits near adults, and significantly fewer at distance; 'repelled' - significantly fewer recruits near adults, with an excess at distance; 'partially repelled' - a peak in recruitment at some intermediate distance, but without a significant decrease in recruits near adults. A final group showed 'no pattern' of varying recruitment probability with distance from adults. The 2 ha seedling study area was too small, and recruitment of dipterocarps over the 2-yr period was too low to allow similar meaningful analysis of the dynamic processes. However, the static patterns of seedlings relative to adults could be described in the terminology of Condit *et al.*(1992). Continuation of measurements

of the marked seedling populations may allow a similar analysis of recruits in the future, at least in the commoner species.

Condit *et al.* (1992) found that the proportion of species with repelled or partially repelled distributions of recruits was greater among large tree species that in the other three groups: medium and small trees, and shrubs. In the seedling study areas, repelled seedling distributions occurred in two species, *S. argentifolia* and *P. malaanonan*, both emergent species. Partially repelled patterns were found in *S. johorensis* and *S. agamii*, emergent and large tree respectively. Attracted seedling distributions occurred in two canopy species, *H. nervosa* and *V. dulitensis*, and the two emergent species of DRM, *S. fallax* and *S. pauciflora*. Two emergent species (*S. leprosula* and *S. parvifolia*), and one canopy species (*V. sarawakensis*) showed no significant pattern.

Difficulties of interpreting seedling patterns

Several aspects of relative dispersion of seedlings and adults were often, but not always, correlated, and are likely to interact in different ways with the processes of growth, mortality and recruitment. These included:

- percentage of seedlings with a conspecific nearest adult (NA)
- local seedling density
- % of conspecific versus heterospecific seedlings beneath adult trees
- region of greatest seedling frequency.

Separation of these aspects can be important in testing hypotheses concerning the escape hypothesis, or compensatory mechanisms (Clark & Clark 1984).

Species which show strongly 'repelled' seedling patterns (*sensu* Hubbell & Foster 1990b) are predicted to have better dispersed adults (Clark & Clark 1984), while those with 'attracted' seedling patterns should have more clumped adults. This was true in some species in Plot 1: *S. fallax* for example had strongly aggregated seedlings and trees. while most of the light-demanding species has less aggregated seedlings and relatively well-distributed adults. Finally, if no evidence for the existence of spacing mechanisms is demonstrated, all that can be inferred is that once seedlings have reached the age, or size, of the youngest (or smallest) seedlings in the population, spacing mechanisms are not operating. It is not possible to infer that they

did not operate on smaller size classes. In the present study, several years after seedfall, the most intense mortality had likely already occurred, and could have resulted in large changes in spatial pattern (Augspurger 1983a).

Lieberman & Lieberman (in press) caution that seedling spatial patterns must be interpreted with caution, especially when factors determining adult spatial pattern are inferred from seedling studies. They quote as an example Clark & Clark's (1984) study of density-dependent mortality in *Dipteryx panamensis*. After two years, no seedlings survived within eight meters of adult trees. However, adult trees are found at densities of only around 2 per hectare, a quite different spatial scale. Adult trees in the eleven dipterocarp species occurred at similar densities: between one and eight per hectare.

CHAPTER 9

CONCLUSIONS

9.1 REVIEW OF TECHNIQUES USED

Size of survey area

The 2 ha area surveyed in Plot 1 was large enough to contain a diverse range of dipterocarp species in terms of adult stature and light demanding status. Most of the species were present with sufficient numbers of adult trees and seedlings to allow investigation of dynamics and pattern. The size of the area has enabled detailed investigation of the large scale patterns of seedling distribution, the spatial relationships between seedlings and adults, and the numerical relationships between trees and both 'advance regeneration' and seedlings. In most species, numbers of individuals were large enough to analyse growth and mortality in separate height classes, and estimates of growth and mortality rates were based on large numbers of individuals. A disadvantage, even in the relatively homogeneous areas of forest chosen, was that great variability was introduced. However, restrictions of time meant that a smaller area of Plot 2, 0.48 ha, was enumerated, and this proved too small for seedling pattern and seedling-adult spatial relationships to be explored in as much detail as in Plot 1. Numbers of seedlings in some species were too low to allow analyses of separate size classes.

The two areas surveyed together contained almost 5000 seedlings, resulting in a large data set. Routines were written in FORTRAN to sort the data, calculate growth and mortality rates and abstract data for further analyses. Most statistical testing was done using statistical packages (SPSS^X and MINITAB) as appropriate. Specially-written FORTRAN routines were necessary in pattern analysis, where standard statistical testing was invalid because the theoretical distributions are not known, and random simulations were used to generate null distributions against which to test the observed data. Use was made of published subroutines and the

random number generating functions provided in the NAG library.

Timing of enumerations

The intervals between enumerations were relatively long and variable in length, and the calculated growth and mortality rates are therefore averaged over six or 18 months. Information was thus lost on the occurrence of events such as short drought periods or the creation of small canopy openings, and their effects on seedling mortality and growth rates. These factors may be especially important in species or size classes with high mortality or growth rates, as these rates were found to fluctuate more over time than in species/size classes with slower rates of growth or mortality. For example, in Plot 1 a branch fall in one 20 x 20 m subplot shaded a group of *S. argentifolia* seedlings, most of which died; this single chance event accounted for 27% of the total mortality of this species over the second interval. More frequent enumeration would have allowed cause of death to be determined with greater certainty, and may for example have revealed a closer link between physical damage and mortality. Similarly, growth rates were calculated from height differences which were the net result of a combination of dormancy, stem breakage, and/or rapid growth. The 'resolution' of the present study was not fine enough to detect rhythmic growth, accurately measure length of dormancy in individual seedlings, detect responses to transient canopy opening, or isolate the fastest growth rates. This did not bias comparisons between species or plots within the study, but may affect comparisons with other studies. For example when comparing maximum growth rates from this study it is important to note that these are averaged over 6 or 18 months, and it is likely that for some period during that time the actual growth rate may have been higher.

Growth and mortality

The definition of 'seedling' in this project was broad, as all individuals up to the lower limit of the tree enumeration, 10 cm gbh, were included. Heights ranged from ca. 8 cm to over 7 m. Because rates of growth and mortality vary greatly with size, species were separated into size classes. In most species, numbers of seedlings were large enough to allow division into six height classes. If the class size becomes

too small, significance testing is impossible, and one chance death would produce a spuriously high estimate of mortality for that class relative to adjacent classes. Recommendations for minimum numbers of individuals for estimates of mortality range from 5 (Connell *et al.* 1984) to 100 as a 'reasonable population size for studies of dynamics' (Manokaran *et al.* 1993). For a class size of 20, and mortality rate of around 5% yr^{-1}, one seedling is expected to die per year, the minimum expected per cell for a chi-squared test. In order to make significance testing worthwhile, a minimum of 20 per class is suggested for the observed range of mortality rates found in the Danum populations.

The distributions of individual growth rates were found to be highly skewed, with many negative increments. Some previous studies have ignored these negative increments as 'aberrant', but the current study has shown the high frequency of height loss in natural seedling populations in rain forest, and the decision was made to include them in the analyses and comparisons. These data could not be normalised by transformation, and therefore non-parametric statistical tests had to be used.

Pattern analysis

Four methods were used to investigate the spatial patterns of seedlings, ranging from a simple single index based on mean nearest neighbour distance with a known statistical distribution, the Clark-Evans test, to Ripley's K(t), a function of the distribution of all inter-seedling distances employing a complex edge correction and requiring simulation methods to generate null distributions against which to test the observed distribution. The results from the four tests agree closely in terms of the rank order of species by degree of aggregation. While the more complex tests provided additional information on the variation in pattern with scale, they also supported the quick and simple Clark-Evans Test as a robust overall assessment of pattern.

Morisita's Index provided a useful description of variation in pattern with scale, and results were similar to those of the more rigorous tests. The Index suffers from the problem that significance testing is not considered appropriate (Hurlbert 1990, see Chapter 7.2.2), but results can be used to suggest hypotheses which could be tested.

Sample size is an important consideration in pattern analysis. The detection

of aggregation can be influenced by density (Greig-Smith 1983): an aggregated species with a small population size could be detected as randomly distributed because of the high variance introduced, while a less-strongly aggregated population with more individuals may be correctly detected as aggregated. A minimum population size of 25 is suggested for meaningful analysis for the range of densities and degrees of aggregation within the Danum seedling populations.

9.2 CORRELATIONS OF PATTERN CHARACTERISTICS AND GROWTH AND MORTALITY RATES

Correlations were examined between spatial distribution of seedlings and rates of mortality and growth, and stature of adult trees in each species. None of the emergent light-demanding, fast-growing species had strongly aggregated seedlings, and in none of these species were seedlings clumped relative to adults. All were either repelled (*S. argentifolia, P. malaanonan*), partially repelled (*S. johorensis*) or showed no pattern (*S. leprosula, S. parvifolia*). Pattern analysis suggested a pattern of small-scale clumping, especially of larger seedlings, combined with more uniform distribution on the scale of the 2 ha plot. Mortality rates in these species were high, especially in small seedlings, (with the exception of *P. malaanonan*), and growth rates could be very fast in all species. These observation suggest that a combination of well-dispersed seeds and initial high mortality in small seedlings leads to well-dispersed and low density seedling populations. These species depend on gap creation for growth (Wyatt-Smith 1966b, Ashton 1982, Whitmore 1984). Since gap creation is spatially unpredictable, it is an obvious advantage if the area is saturated with seedlings, but at low density to minimise intra-specific competition when a gap is created. Large seedlings in these species were more clumped than small seedlings, possibly because large seedlings are (or were) in small canopy gaps. In these species, it is suggested that the initial seed shadow pattern is only weakly aggregated due to relatively efficient seed dispersal, and aggregation is further weakened by high mortality. Gap creation then imposes a secondary pattern on seedling distribution.

S. johorensis seedlings were intermediate between the LRMs and DRMs in both growth and mortality rates, and in degree of aggregation. This species has been

noted to form a seedling bank, and mortality and growth rates were relatively high.

In Dark Red Merantis, seedlings were strongly aggregated around adult trees, suggesting that seed dispersal is more limited. The two species were very similar in all aspects of pattern. In both species, small seedlings were more clumped than large. However, they differed in growth and mortality profiles. Mortality in *S. pauciflora* was higher than in *S. fallax*, and varied more with size: in *S. fallax* mortality was constant throughout the seedling size range, a characteristic shared with *P. malaanonan* in Plot 1. The *S. fallax* population contained a high proportion of large saplings, many appearing to be of low vigour: girth was large relative to height, apical dominance had been lost, and many had multiple small orthotropic shoots arising from lower down the stem. This contrasts with the high vigour of smaller seedlings, especially in Plot 2, where growth rates were higher than in many of the LRM.

Fox (1972) states that: 'the less common *Rubroshoreas* can remain constituents through wider dispersal of fewer seed, and greater seedling persistence'. In contrast, evidence from the present study suggests that the *Shorea* species with widely dispersed seedlings had low persistence, while the strongly aggregated species had higher persistence.

P. malaanonan seedlings combined high growth rates with low mortality rates, and had widely-dispersed seedlings. The most extremely 'repelled' seedling pattern was in *P. malaanonan*, and the proportion of small seedlings was relatively high. Very strong differential mortality could produce such a repelled pattern. However, examination of the dispersion map of *P. malaanonan* (Appendix 3) reveals that the four adult trees occur at the north end of the study area, while the seedlings are generally found towards the south, suggesting the alternative explanation that the species may be invading the study area from the north. From the spatial pattern and size distribution of *S. leprosula* at Jengka in Peninsular Malaysia, Poore (1969) concluded that this species had invaded the area relatively recently.

Canopy trees occurred at low densities (one or two per hectare, trees over 80 cm gbh). Seedling pattern was random, and distribution relative to adults showed no variation in numbers with distance in one species, *V. sarawakensis*, but in the remaining two species, seedlings were strongly aggregated with respect to adults (*V. dulitensis, H. nervosa*). Seedlings in this group generally had low mortality rates; the 1985 cohort of *V. dulitensis* seedlings was an exception, but mortality in older seedlings was low.

9.3 SUMMARY OF EVIDENCE FOR EQUILIBRATING FORCES

Evidence for the existence of density dependent mechanisms, the Janzen-Connell model and the compensatory mechanisms of Connell *et al.* was sought in both static and dynamic patterns and is summarised below.

Positive evidence

- Increased seedling mortality near conspecific adults was shown in the two species in Plot 1 with highest adult basal area. The two species were also ranked higher for mortality and lower for growth relative to other, less abundant species.
- There was a significant relationship across species between seedling mortality rates and basal area of adult trees. This relationship held in both plots.
- Between plots, seedling mortality was usually higher in the plot where density was highest. This applied to both seedling numbers and adult basal area. In some species, larger seedlings were more uniformly spaced than small, consistent with a prediction of the model.
- Trees were usually more uniformly spaced than seedlings of the same species. However, this occurred in trees of all species pooled, suggesting physical crowding or crown interaction as an alternative (Lieberman & Lieberman, in press).
- Larger seedlings were significantly further from adults than smaller seedlings in two species in Plot 1.
- One of the strongest tests was the change in dispersion of seedlings relative to adults. In Plot 1, median seedling-to-adult distances increased significantly over the survey period in two species: *S. leprosula* and *S. pauciflora*.

Negative evidence

In the clearest test, the changes in seedling-to-adult distance in a single cohort of *V. dulitensis* seedlings beneath the parent tree, the evidence was against the model: median seedling-to-adult distances actually decreased over time, because of higher mortality further from the adult.

In summary, the best evidence for the Janzen-Connell model came from *S. pauciflora*, characterised by high basal area, large-sized adult trees and strongly aggregated seedlings. However, the significantly higher mortality beneath conspecific

adults in *S. pauciflora* did not produce a repelled (static) seedling pattern over the study period, that is, there were still significantly more seedlings than expected near to the adults. Seedlings were still strongly aggregated, but mean seedling-to-adult distance was significantly higher at the end of the study period, and there was a significant trend of increasing median seedling-to-adult distance with increasing size of seedling.

Evidence from both static (variation in distance with height) and dynamic (variation in distance over time) patterns indicates that significant increase in spacing is occurring, consistent with the Janzen-Connell model, but this has not led to a reduction of seedling numbers near adults below expectation. Numbers of large (>250 cm) saplings beneath adult trees were higher than expected (Table 8.7), emphasising that clumping *per se* does not rule out the existence of spacing mechanisms (Clark & Clark 1984). This underlines the importance of following the dynamic aspects of pattern over time. Although the present distribution of seedlings is strongly aggregated, it is more uniform than the initial seedling dispersion pattern. Conversely, significantly repelled seedling patterns occurred in species in which differential mortality was not demonstrated: *S. argentifolia* and *P. malaanonan*. The most intense mortality may already have occurred in these species, since even the smallest seedlings were assumed to be at least four years old. While there was no evidence from dynamic or static pattern analysis that spacing mechanisms are operating in these species, their existence in the past cannot be ruled out (Clark & Clark 1984).

Many of the characteristics which should promote species co-existence under the 'storage effect' hypothesis of Chesson & Warner (1981) have been demonstrated in the present dipterocarp populations. These include low adult mortality (Chapter 6), the presence of persistent 'stored' seedlings in the population (Chapter 2), varying mortality rates in seedlings (Chapter 3.3.1), with the possibility that species varied in their responses to the dry season (Chapter 3.3.3). The contribution of storage to species persistence and co-existence could be quantified (Warner & Chesson 1985) if long-term data on variation in recruitment between species were available. This should include phenological data - some species, often canopy species (Ashton 1988a) are known to flower in years between mast fruiting of emergent trees, and may be able to store seedlings from these times.

The positive correlation of seedling rates of growth and mortality across

species, and the correlation of seedling mortality rates with basal area of conspecific adults, both suggest compositional equilibrium. The significant relationships between numbers of trees and of seedlings and 'advance regeneration' suggest the continuing abundance of the major species.

9.4 IS FOREST IN DANUM IN A LATE STAGE OF RECOVERY FROM MAJOR DISTURBANCE?

The importance of rare, major exogenous disturbance in tropical forests is recognised (Whitmore 1984, Clark 1986). A drought occurred in Sabah in 1915 (Whitmore 1984), and more recently, the drought in 1983 caused widespread fires in undisturbed forest across Borneo (Beaman *et al.* 1985, Woods 1985). Evidence from the structure of the Danum forest led Newbery *et al.* (1992) to suggest that the forest is in the later stages of recovery from 'moderate disturbance some decades previously'. The evidence includes the low basal area, and fewer large trees than comparable sites (Newbery *et al.* 1992). Pioneer trees occur at low density, and the pioneer seed bank is low (Kennedy 1990, Kennedy & Swaine 1992). Gap frequency seems low compared to other forests: Brokaw (1985b), in a review of gap frequency and area in other studies of tropical forests found that gap area ranged from 3-15% of forest area, although definitions of gaps varied between workers. In the two 4 ha plots, gaps formed 0.52% and 0.46% of plot area (Newbery *et al.* 1991). In a survey of 10 ha near the two plots, 0.3-0.5% of forest was in gap phase (Brown 1990). In the same review Brokaw found gap sizes to range from 100 - 600 m^2. In the two 4 ha plots, mean gap area was 23 m^2, with 95% confidence limits of 13 m^2-40 m^2 (Newbery *et al.* 1992). In other areas of the Danum forest, gaps were smaller: 70% were less than 30 m^2 and 44% were smaller than 10 m^2 (Brown 1990). These observations suggest that currently the Danum forest is in a mature, closed canopy phase.

Is there any evidence from the dipterocarp seedling enumeration to support this, in terms of seedling densities, species composition or height structure? A combination of dense canopy, low frequency of small gaps, resulting in few opportunities for rapid seedling growth, and length of time (at least four years) since

last mast fruiting, lead to the prediction that the numbers of dipterocarp seedlings, particularly of the light-demanding species, should be low. In the seedling study areas, densities were between 2000 and 2500 seedlings per hectare, much lower than other figures quoted for Sabah (Fox 1967, 1972, Liew & Wong 1973) which are in the order of tens of thousands. Alternatively, the exceptional drought in 1983, and absence of fruiting since, may be the cause of the low numbers of dipterocarp seedlings observed. Seedlings of the light-demanding species were relatively abundant, forming 44% of the seedling populations (mean of the two study areas). Most species had a large proportion of tall seedlings (over 2.5 m). Proportions of tall seedlings were relatively high in the light-demanding Light Red Merantis, suggesting that under the prevailing, or relatively recent, canopy conditions, they were able to grow tall.

A consequence of lower rates of disturbance is smaller and fewer gaps, which are likely to be more transient, and more likely to be infilled by growth of surrounding trees (Denslow 1987). It is likely that the opportunity for increased growth of seedlings will be short-lived. Growth of saplings into the canopy may therefore be in several stages, with height growth ceasing as each small gap grows over. Evidence from growth simulation (Chapter 4.11), the increased mortality in medium-sized seedlings of fast-growing species (especially LRMs) (Chapter 3.4) and higher auto-correlation of growth rates in fast-growing species (Chapter 4.9) suggests that fast-growing species may be less tolerant of 'stop-start' growth than more slow-growing species, and are unable to tolerate periods of dormancy after release. The maximum growth rates recorded in saplings of LRMs suggest that they could reach the canopy in a few years. It seems likely that, while seedlings of LRMs are released by, and show strong growth responses to, even very small canopy openings, larger gaps are necessary to sustain growth up to the canopy. Perhaps a larger gap is required for successful regeneration, not because available light is greater than in a small gap, or that a larger gap is required for release, but because a large gap is likely to last longer, enabling upward growth to continue for longer, and increasing the chance of reaching the canopy.

A large proportion of seedlings had evidence of past stem breakage or damage. Litter-fall caused 12% of seedling deaths, likely to be an under-estimate, because the length of the inter-census intervals may have limited detection. This frequency seems lower than figures from neo-tropical forests (see references in

Chapter 3) and may be associated with lower rates of canopy disturbance. Nevertheless, seedlings are at high risk from physical damage caused by branch-falls. In slow growing species, it appeared that damage accumulated over time, and growth rates were not fast enough to enable recovery. The price for persistence in these species is the constant risk of damage from falling debris.

9.5 FUTURE WORK

It will be of great interest to follow the fate of the existing marked seedlings. Mortality in the dipterocarp seedling populations is relatively low (compare for example Li 1990), and a large proportion are expected to be still alive. Projecting from the second interval mortality rate in Plot 1, 2410 seedlings out of the population surviving to July 1988 of 3179 (excluding the 1985 *V. dulitensis* cohort) are predicted to be alive at the end of 1992. In Plot 2, the prediction is 714 out of 912. Numbers of surviving seedlings in each species are likely to be sufficient to allow continued monitoring of growth rates and comparisons between species. Direct observation of a mast fruiting event will allow seed-fall patterns to be described, and new cohorts of seedlings could be followed from germination, allowing a more rigorous test of the Janzen-Connell hypothesis. How do newly-germinating seedlings interact with established seedlings, especially in species with clumped seedlings?

It would be useful to compare growth rates immediately after germination, and in very young seedlings in different species. Wyatt-Smith (1958) suggested that seedlings of some dipterocarp species require a gap within ten years of germination. Do the successful seedlings come from the seedling bank of suppressed individuals or from more recently germinated seedlings? Is the ability to be released lost or reduced as the seedling ages? The present study suggested that LRM seedlings may be less tolerant of a reduction in growth rate after release. They also showed large increases in growth rate in response to small canopy openings resulting from branch-falls. In a regime in which small canopy gaps predominate, as seems to be the case in Danum forest at the present time, shade-tolerant species might be predicted to be more successful. While the LRMs can respond strongly to even very small canopy openings, these are more likely to be infilled by lateral growth of surrounding

trees, and LRM seedlings may be less able to survive a further period of suppression. However, proportions of LRMs are currently relatively high, and tall seedlings are common. Longer-term and more regular enumerations are required to answer many of these questions.

Long-term observations will also allow the dynamic aspects of spatial pattern to be studied. Where are recruits found, relative to adult trees? The relationship between static dispersal patterns and long-term recruitment patterns remains to be investigated. Ideally single cohorts of seedlings should be monitored from germination until they reach reproductive maturity, which would require decades. The minimum time for suppressed seedlings in this study to reach 5 m tall was estimated from Growth Simulation to range from 11-45 years in different species. Extrapolating from the fastest observed individual growth rates, the time to reach 20 m height could range from 9-53 years. The current patterns of adult trees are the outcomes of environmental, biotic and chance factors operating over very many years. Such long term monitoring may reveal the impact of 'rare' events on forest dynamics and compositional stability, for example the effects of 'El Niño' oscillations, and the possible cyclical nature of the endogenous disturbance regime. Manokaran's (1988) long-term study of changes in lowland dipterocarp forest over 38 years showed that tree species composition was essentially stable despite more than half the trees dying and being replaced. In saplings, changes in composition and population size were much greater. The marked seedling populations afford an opportunity to follow spatial dynamics and changes in composition of seedlings in a relatively large area.

Detailed monitoring of environmental variables is required to try to explain some of the variation in growth, especially, and mortality. Water stress may be important in mortality regimes (Becker 1983a) and was thought to be a factor in the increased mortality of some species over the second interval in the present study. In view of the great importance of light gaps to dipterocarp seedlings, a deficiency in this study is the lack of light measurements. Light measurements taken over a random selection of seedlings could be related to growth. Individual measurement such as this have rarely been attempted (eg Pearcy 1983, Chazdon & Fetcher 1984, Oberbauer *et al.* 1988). One of the problems is scale - simultaneous measurement of light are required if comparison between individuals is to be made. Hemispherical photographs taken immediately above each seedling would permit the available light to be accurately quantified. This is possible in small seedlings, but becomes more

difficult in larger saplings. Light measurements or photographs must be repeated over time to trace small changes in canopy openness, to attempt to relate these to changes in growth rate. Other approaches to quantify the light environment address these problems. The canopy closure method of Lieberman *et al.* (1989) estimates the extent of shading from the heights of surrounding, larger trees. A recent study by Clark & Clark (1992) compares sapling performance and evaluates the light microsite in terms of the number of over-topping crowns, crown illumination index and forest phase. The problems of acquiring a large enough sample size in diverse rain forest are also illustrated by this study - 150 ha of forest were searched to find sufficient numbers of individuals of six non-pioneer species in the chosen size classes and microhabitat conditions.

Replication of plots is important: do species behave in the same way wherever they occur? This study showed that some species had different mortality or growth rates between the two plots in for example. Replication is required to compare the relative performance of species under a range of conditions. Differences in seedling mortality rates across species between the two plots suggested a relationship with density of conspecific adult, but this could not be rigorously tested. In searching for evidence for density- or distance-dependent spacing mechanisms as predicted by Janzen (1970) and Connell (1971), further insight can be gained if species are studied over a range of abundance.

CHAPTER 10

REFERENCES

AIDE T. M. 1987. Limbfalls: A major cause of sapling mortality for tropical forest plants. *Biotropica* 19: 284-285.

ALEXANDER I., AHMAD N. & SEE L.S. 1992. The role of mycorrhizas in the regeneration of some Malaysian forest trees. *Phil. Trans. R. Soc. Lond. B* 335: 379-388.

APPANAH S. & CHAN H.T. 1981. Thrips: the pollinators of some dipterocarps. *Malay. Forester* 44: 234-252.

ARMESTO J. J. MITCHELL J. D. & VILLIGRAN C. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18: 1-11.

ASHTON P.S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* 1: 155-196.

ASHTON P.S. 1982. Dipterocarpaceae. *Flora Malesiana Ser. I.* 9: 237-552.

ASHTON P.S. 1988a. Dipterocarp reproductive biology. In: *Tropical Forest Ecosystems. B. Biogeographical and Ecological Studies.* Eds. Leith H.& Werger M.J.A. Elsevier, Amsterdam, The Netherlands.

ASHTON P.S. 1988b. Dipterocarp biology as a window to the understanding of tropical forest structure. *Ann. Rev. Ecol. Syst.* 19: 347-370.

AUBRÉVILLE A. 1938. La fôret coloniale: les fôrets de l'Afrique occidentale française. *Ann. Acad. Sci. Colon.* 9: 1-145.

AUGSPURGER C.K. 1983a. Seed dispersal of the tropical tree, *Platypodium elegans,* and the escape of its seedlings from fungal pathogens. *J. Ecol.* 71: 759-771.

AUGSPURGER C.K. 1983b. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189-196.

AUGSPURGER C.K. 1984a. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J. Ecol.* 72: 777-795.

AUGSPURGER C.K. 1984b. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology* 65: 1705-1712.

AUGSPURGER C.K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *Am. J. Bot.* 73: 353-363.

AUGSPURGER C.K. & FRANSON S.E. 1987. Wind dispersal of artificial fruits varying in mass, area, and morphology. *Ecology* 68: 27-42.

AUGSPURGER C.K. & KELLY C.K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61: 211-217.

BARNARD G.A. 1963. Discussion of the paper by Prof. M.S. Bartlett. *J. Roy. Statis. Soc.* 3: 185-194.

BARNARD R.C. 1956. Recruitment, survival and growth of timber-tree seedlings in natural tropical forest. *Malay. Forester* 19: 156-161.

BAUR G.N. 1964. Rainforest treatment. *Unasylva* 18: 18-28.

BAZZAZ 1984. Dynamics of wet topical forests and their species strategies. In: *Physiological Ecology of Plants of the Wet Tropics*. Eds. Medina E., Mooney H.A. & Vasquez-Yanes C. Dr W. Junk, The Hague, The Netherlands.

BEAMAN R.S., BEAMAN J.H., MARSH C.W. & WOODS P.V. 1985. Drought and forest fires in Sabah in 1983. *Sabah Society Journal* 8: 10-30.

BECKER P. 1983a. Effects of insect herbovory and artificial defoliation on survival of *Shorea* seedlings. In: *The Tropical Rain Forest: Ecology and Management*. Eds. Sutton S.J., Whitmore T.C. & Chadwick A.C., Blackwell Scientific Publications, Oxford, UK.

BECKER P. 1983b. Ectomycorrhiza on *Shorea* (Dipterocarpaceae) seedlings in a lowland Malaysian Rainforest. *Malay. Forester* 46: 146-164.

BECKER P. & WONG M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia sp.* (Meliaceae) in lowland dipterocarp rainforest. *Biotropica* 17: 230-237.

BECKER P., LESTER L.W., ROTHMAN E.D., & HAMILTON W.D. 1985. Seed predation and the coexistence of tree species: Hubbell's models revisited. *Oikos* 44: 382-390.

BESAG J. 1977. Contribution to discussion. *J. Roy. Statis. Soc. B* 39: 77-92.

BROKAW N.V.L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158-160.

BROKAW N.V.L. 1985a. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682-687.

BROKAW N.V.L. 1985b. Treefalls, regrowth, and community structure in tropical forests. In: *The Ecology of Natural Disturbance and Patch Dynamics.* Eds. Pickett S.T.A. & White P.S. Academic Press, New York, USA.

BROWN N. 1990. *Dipterocarp Regeneration in Tropical Rain Forest Gaps of Different Sizes.* PhD Thesis, University of Oxford.

BROWN N. & WHITMORE T.C. 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? *Phil. Trans. R. Soc. Lond. B.* 335: 369-378.

BROWN W.H. & MATHEWS D.M. 1914. Philippine dipterocarp forests. *Phil. J. Science* 9: 413-561.

BURGESS P.F. 1966. Timbers of Sabah. *Sabah Forest Records No. 6.* Forest Department, Sabah, Malaysia.

CALDWELL M.M. 1987. Plant architecture and resource competition. In: *Potentials and limitations of ecosystem analysis.* Eds. Schulze E.D. & Zwolfer H. Ecological Studies Vol 61. Springer-Verlag, Berlin, Germany.

CHAN H.T. 1980. Reproductive biology of some Malaysian Dipterocarps II. Fruiting biology and seedling studies. *Malay. Forester* 43: 438-451.

CHAN H.T. 1981. Reproductive biology of some Malaysian Dipterocarps III. Breeding systems. *Malay. Forester* 44: 28-36.

CHAN H.T. & APPANAH S. 1980. Reproductive biology of some Malaysian Dipterocarps I. Flowering biology. *Malay. Forester* 43: 132-143.

CHAZDON R.L. & FETCHER N. 1984. Photosynthetic light environments in a lowland rain forest in Costa Rica. *J. Ecol.* 72: 553-564.

CHESSON P.L. & WARNER R.R. 1981. Environmental variability promotes coexistence in lottery competitve systems. *Am. Nat.* 117: 923-943.

CLARK D.A. 1986. Regeneration of canopy trees in tropical wet forests. *TREE* 1: 150-154.

CLARK D.A. & CLARK D.B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell Model. *Am. Nat.* 124: 769-788.

CLARK D.A & CLARK D.B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.* 62: 315-344.

CLARK D.B. 1990. The role of disturbance in the regeneration of neotropical moist forests. In: *Reproductive ecology of tropical forest plants.* Eds. Bawa K.S. & Hadley M. Man and the Biosphere Series Vol. 7, UNESCO/IUBS, Paris and Parthenon Publishing, Carnforth, UK.

CLARK D.B. & CLARK D.A. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66: 1884-1892.

CLARK D.B. & CLARK D.A. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica* 19: 236-244.

CLARK D.B. & CLARK D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225-230.

CLARK P.J. & EVANS F.C. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* 35: 445-453.

CONDIT R., HUBBELL S.P. & FOSTER R.B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am. Nat.* 140: 261-286.

CONNELL J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of populations*. Proceedings of the Advanced Study Institute. Eds. den Boer, P.J. & Gradwell G.R., Wageningen, The Netherlands.

CONNELL J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.

CONNELL J.H. & SLATYER R.O. 1987. Mechanisms of succession in natural communities and their role in community stability and organisation. *Am. Nat.* 111: 1119-1144.

CONNELL J.H., TRACEY J.G. & WEBB L.J. 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. *Ecol. Monog.* 54: 141-164.

COOK R.E. 1979. Patterns of juvenile mortality and recruitment in plants. In: *Topics in plant population biology*. Eds. Solbrig O.T., Jain S., Johnson G.B. & Raven P.H. Comlumbia University Press, New York, USA.

DAVID F.N. & MOORE P.G. 1954. Notes on contagious distributions in plant populations. *Annals of Botany* 18: 47-53.

DE STEVEN D. & PUTZ F.E. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43: 207-216.

DENSLOW J.S. 1980. Gap partitioning among tropical rain forest trees. In: Tropical Succession. Ed. Ewel J. *Biotropica* 12 (Supplement): 47-55.

DENSLOW J.S. 1987. Tropical rain forest gaps and tree diversity. *Ann. Rev. Ecol. Syst.* 18: 432-451.

DIGGLE P.J. 1979. Statistical methods for spatial point patterns in ecology. In: *Spatial and Temporal Analysis in Ecology*. Eds. Cormack R.M. & Ord J.K. Maryland, USA.

DIGGLE P.J. 1983. *Statistical analysis of spatial point patterns.* Academic Press, London, UK.

DONNELLY K. 1978. Simulation to determine the variance and edge-effect of total nearest neighbour distance. In: *Simulation Methods in Archaeology.* Ed. Hodder I. Cambridge University Press, London, UK.

DRANSFIELD J. 1978. Growth forms of rain forest palms. In: *Tropical Trees as Living Systems.* Eds. Tomlinson P.B. & Zimmerman M.H. Cambridge University Press, London, UK.

DUNCAN R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. *J. Ecol.* 79: 1073-1084.

FORMAN R.T. & HAHN C.D. 1980. Spatial patterns of trees in a Caribbean semi-evergreen forest. *Ecology* 61: 1267-1274.

FOSTER S.A. & JANSON C.H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 566: 773-780.

FOX J.E.D. 1967. An enumeration of lowland dipterocarp forest in Sabah. *Malay. Forester* 30: 263-279.

FOX J.E.D. 1972. *The natural vegetation of Sabah and natural regeneration of the dipterocarp forests.* Ph.D. Thesis, University of Wales.

FOX J.E.D. 1973. Dipterocarp seedling behaviour in Sabah, Malaysia. *Malay. Forester* 36: 205-214.

FRANKLIN J., MICHAELSON J. & STRAHLER A.H. 1985. Spatial analysis of density dependent pattern in coniferous forest stands. *Vegetatio* 64: 29-36.

GARTNER B.L. 1989. Breakage and regrowth of *Piper* species in rain forest understorey. *Biotropica* 21: 303-307.

GARWOOD N.C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecol. Monog.* 55: 159-181.

GETIS A. & FRANKLIN J. 1987. Second-order neighborhood analysis of mapped point patterns. *Ecology* 68: 473-477.

GREEN D.S. 1980. The terminal velocity and dispersal of spinning samaras. *Amer. J. Bot.* 67: 1218-1224.

GREIG-SMITH P. 1952a. Use of random and contiguous quadrats in the study of the structure of plant communities. *Ann. Bot.* 16: 293-316.

GREIG-SMITH P. 1952b. Ecological observations on degraded and secondary forests in Trinidad, British West Indies. II. Structure of the communities. *J. Ecol.* 40: 316-330.

GREIG-SMITH P. 1979. Pattern in vegetation. *J. Ecol.* 67: 755-779.

GREIG-SMITH P. 1983. *Quantitative Plant Ecology.* Third Edition. Blackwell Scientific Publications, Oxford, UK.

GRUBB P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.

HALL J.B. & SWAINE M.D. 1981. *Distribution and Ecology of Vascular Plants in a Tropical Rainforest. Forest Vegetation in Ghana.* W. Junk, The Hague, The Netherlands.

HAMILL D.N. & WRIGHT S.J. 1986. Testing the dispersion of juveniles relative to adults: a new analytic method. *Ecology* 67: 952-957.

HARPER J.L. 1977. *Population biology of plants.* Academic Press, New York, USA.

HARPER J.L. & WHITE J. 1974. The demography of plants. *Ann. Rev. Ecol. Syst.* 5: 419-463.

HARTSHORN G.S. 1978. Tree falls and tropical forest dynamics. In: *Tropical Trees as Living Systems.* Eds. Tomlinson P.B. & Zimmerman M.H. Cambridge University Press, London, UK.

HILL M.O. 1973. The intensity of spatial pattern in plant communities. *J. Ecol.* 61: 225-235.

HO C.C., NEWBERY D.McC. & POORE M.E.D. 1987. Forest composition and inferred dynamics in Jengka Forest Reserve, Malaysia. *J. Trop. Ecol.* 3: 25-56.

HOWE H.F. & SMALLWOOD J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.

HOWE H.F. & WRIGHT S.J. 1986. Spatial pattern and mortality in the desert mallow (*Sphaeralcea ambigua*). *Nat. Geogr. Res.* 2: 491-499.

HUBBELL S.P. 1979. Tree dispersion, abundance, and diversity in tropical dry forest. *Science* 203: 1299-1309.

HUBBELL S.P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214-229.

HUBBELL S.P. 1984. Methodologies for the study of the origin and maintenance of tree diversity in tropical rain forest. In: *The Significance of Species Diversity in Tropical Forest Ecosystems.* Biology International Special Issue No 6. Eds. Maury-Lechon G., Hadley M. & Younes T. IUBS, Paris, France.

HUBBELL S.P. & FOSTER R.B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: *The Tropical Rain Forest: Ecology and Management.* Eds. Sutton S.J, Whitmore T.C. & Chadwick A.C. Blackwell Scientific Publications, Oxford, UK.

HUBBELL S.P. & FOSTER R.B. 1986a. Biology, chance, and history and the structure of tropical rain forest tree communities. In: *Community Ecology.* Eds. Diamond J. & Case T.C. Harper & Row, New York.

HUBBELL S.P. & FOSTER R.B. 1986b. Canopy gaps and the dynamics of a neotropical forest. In: *Plant Ecology.* Ed. Crawley M.D. Blackwell Scientific Publications, Oxford.

HUBBELL S.P. & FOSTER R.B. 1987. The spatial context of regeneration in a neotropical forest. In: *Colonization, Succession and Stability.* Eds. Crawley M., Gray A. & Edwards P.J. Blackwell Scientific Publications, Oxford, UK.

HUBBELL S.P. & FOSTER R.B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. In: *Reproductive ecology of tropical forest plants.* Eds. Bawa K.S. & Hadley M. Man and the Biosphere Series 7, Vol. 7, UNESCO/IUBS, Paris and Parthenon Publishing, Carnforth, UK.

HURLBERT S.H. 1990. Spatial distribution of the montane unicorn. *Oikos* 58: 257-271.

JANOS D.P. 1980. Vesicular-arbuscular myorrhizae affect lowland tropical rain forest plant growth. *Ecology* 61: 151-162.

JANZEN D.H. 1970. Herbivores and the number of tree species in tropical forests. *Amer. Nat.* 104: 501-528.

JONES E.W. 1955. Ecological studies on the rain forest of southern Nigeria. IV. The plateau forest of the Okumo forest reserve. *J. Ecol.* 43: 564-594.

KENKEL N.C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.

KENNEDY D.N 1990. *The Role of Colonising Species in the Regeneration of Dipterocarp Rain Forest.* Ph.D. Thesis, University of Aberdeen.

KENNEDY D.N. & SWAINE M.D. 1992. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Phil. Trans. R. Soc. Lond. B* 335: 357-366.

KITAJIMA K. & AUGSPURGER C.K. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor. Ecology* 70: 1102-1114.

KOCHUMMEN K.M. 1978. Natural plant succession after farming at Kepong. *Malay. Forester* 41: 76-77.

KOCHUMMEN K.M. & LaFRANKIE J.V. 1990. Stand structure of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *J. Trop. For. Sci.* 3: 14-24.

KOCHUMMEN K.M., LaFRANKIE J.V. & MANOKARAN N. 1990. Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *J. Trop. For. Sci. 3*: 1-13.

LANG G.E., KNIGHT D.H. & ANDERSON D.A. 1971. Sampling the density of tree species with quadrats in a species-rich tropical forest. *Forest Sci.* 17: 395-400.

LI M. 1991. *The ecology of neotropical tree seedlings.* Ph.D. Thesis, University of North Dakota, Grand Forks, North Dakota, USA.

LIEBERMAN D., LIEBERMAN M., HARTSHORN G.S. & PERALTA R. 1985a. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *J. Trop. Ecol. 1*: 97-109.

LIEBERMAN D., LIEBERMAN M., PERALTA R. & HARTSHORN G.S. 1985b. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* 73: 915-924.

LIEBERMAN M. & LIEBERMAN D. 1985. Simulation of growth curves from periodic increment data. *Ecology 66*: 632-635.

LIEBERMAN M. & LIEBERMAN D. *In press.* Patterns of density and dispersion of forest trees. In: *La Selva: Ecology and Natural History of a Neotropical Rainforest.* Eds. McDade L.A. Bawa K.S., Hespenheide H.A. & Hartshorn G.S. University of Chicago Press, Chicago, USA.

LIEBERMAN M., LIEBERMAN D. & PERALTA R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forest. *Ecology* 70: 550-552.

LIEW T.C. & WONG F.O. 1973. Density, recruitment, mortality and growth of Dipterocarp seedlings in virgin and logged-over forests in Sabah. *Malay. Forester* 36: 3-15.

LLOYD M. 1967. Mean crowding. *J. Anim. Ecol.* 36: 1-30.

MANOKARAN N. 1988. *Population dynamics of tropical forest trees.* Ph.D. Thesis, University of Aberdeen.

MANOKARAN N. & KOCHUMMEN K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol.* 3: 315-330.

MARSH C.W. & GREER A.G. 1992. Forest land-use in Sabah, Malaysia: an introduction to the Danum Valley. *Phil. Trans. R. Soc. Lond. B* 335: 327-330.

MEIJDEN E. van der, WIJN M. & VERKAAR H.J. 1987. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355-363.

MEIJER W. & WOOD G.H.S. 1964. Dipterocarps of Sabah (North Borneo). *Sabah Forest Record No. 5.* Forest Department, Sandakan, Sabah, Malaysia.

MORISITA M. 1959. Measuring of the dispersion of individuals and the analysis of the distributional patterns. *Memoirs of the Faculty of Science, Kyushu University* 2: 215-235.

MYSTER R.W. & McCARTHY B.C. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56: 145-148.

NAG 1980. *FORTRAN Library Manual* Mark 8. Numerical Algorithms Group, Oxford.

NEWBERY D.McC, CAMPBELL E.J.F., LEE, Y.F., RIDSDALE C.E. & STILL M.J. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Phil. Trans. R. Soc. Lond. B* 335: 341-356.

NEWBERY D.McC., RENSHAW E. & BRUNIG E.F. 1986. Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio* 65: 77-89.

NEYMAN J. & SCOTT E.L. 1972. Processes of clustering and applications. In: *Stochastic point processes.* Eds. Lewis P.A.W. Wiley, New York, USA.

NG F.S.P. 1976. Responses to leader-shoot injury in *Shorea platyclados. Malay. Forester* 39: 91-100.

NG F.S.P. 1981. Vegetative and reproductive phenology of dipterocarps. *Malay. Forester* 44: 197-221.

NICHOLSON D.I. 1960. Light requirements of seedlings of five species of Dipterocarpaceae. *Malay. Forester* 23: 344-356.

NICHOLSON D.I. 1965a. A review of natural regeneration in the Dipterocarp forests of Sabah. *Malay. Forester* 28: 4-24.

NICHOLSON D.I. 1965b. *A study of virgin forest near Sandakan, North Borneo.* Symposium on ecological research in humid tropical vegetation. UNESCO/Government of Sarawak. Kuching, Sarawak, Malaysia.

NUNEZ-FARFAN J. & DIRZO R. 1988. Within-gap spatial heterogeneity and seedling performance in a Mexican tropical forest. *Oikos* 51: 274-284.

OBERBAUER S.F. & STRAIN B.R. 1985. Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosaceae) in Costa Rica. *J. Trop. Ecol.* 1: 303-320.

OBERBAUER S.F., CLARK D.B., CLARK D.A. & QUEDASA M. 1988. Crown light environments of saplings of two species of rain forest emergent trees. *Oecologia* 75: 207-212.

PEMADASA M.A. & GUNATILLEKE C.V.S. 1981. Pattern in a rain forest in Sri-Lanka. *J. Ecol.* 69: 117-124.

PICKETT S.T.A. 1983. Differential adaptation of tropical tree species to canopy gaps and its role in community dynamics. *Trop. Ecology 24*: 68-84.

PIELOU E.C. 1969. *An introduction to Mathematical Ecology.* Wiley, New York, USA.

PIELOU E.C. 1977. *Mathematical Ecology.* Wiley, New York, USA.

PINDER D.A. & WITHERICK M.E. 1972. The principles, practice and pitfalls of nearest neighbour analysis. *Geography* 57: 277-288.

PINERO D.A. & MARTINEZ-RAMOS M. & SARUKHAN J. 1984. A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *J. Ecol.* 72: 977-991.

PLATT W.J., EVANS G.W., & RATHBURN S.L. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *Amer. Nat.* 131: 491-525.

POORE M.E.D. 1968. Studies in Malaysian rainforest. I. The forest on Triassic sediments in Jengka Forest Reserve. *J. Ecol.* 56: 143-196.

PUTZ F.E. & BROKAW N.V.L. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* 70: 508-512.

PUTZ F.E. & MILTON K. 1982. Tree mortality rates on Barro Colorado Island. In: *The Ecology of a Tropical Forest: Seasonal rhythms and long-term changes.* Eds. Leigh E.G., Rand A.S. & Windsor D.M. Smithsonian Institute Press, Washington, D.C., USA.

RAICH J.W. & CHRISTENSEN N.L. 1989. Malaysian dipterocarp forests: tree seedling and sapling species composition and small-scale disturbance patterns. *Nat. Geog. Res.* 5: 348-363.

RAO P.B. & SINGH S.P. 1985. Population dynamics of a foot-hill sal (*Shorea robusta* Gaertn. f.) forest in Kumaun Himalaya. *Acta Oecologica/Oecologia Plantarum* 6: 147-152.

READ J. & HILL R.S. 1985. Dynamics of *Nothofagus*-dominated rainforest on mainland Australia and lowland Tasmania. *Vegetatio* 63: 67-78.

RICHARDS P.W. 1952. *The Tropical Rain Forest.* Cambridge University Press, Cambridge, UK.

RICHARDS P.W. 1969. Speciation in the tropical rain forest and the concept of the niche. *Biol. J. Linn. Soc.* 1: 149-153.

RICHARDS P. & WILLIAMSON G.B. 1975. Treefalls and patterns of understorey species in wet lowland tropical forest. *Ecology* 56: 1226-1229.

RIDLEY H.N. 1930. *Dispersal of plants throughout the world.* Reeve, Ashford.

RIPLEY B.D. 1976. The second-order analysis of stationary point processes. *J. Appl. Prob.* 13: 255-266.

RIPLEY B.D. 1977. Modelling spatial patterns. *J. Roy. Stat. Soc. B* 39: 172-212.

RIPLEY B.D. 1978. Spectral analysis and the analysis of pattern in plant communities. *J. Ecol.* 66: 965-981.

RIPLEY B.D. 1979. Tests of "randomness" for spatial point patterns. *J. Roy. Stat. Soc. B* 41: 368-374.

RIPLEY B.D. 1981. *Spatial Statistics.* Wiley, New York, USA.

RIPLEY B.D. 1986. Spatial point pattern analysis in ecology. In: *Developments in numerical ecology.* Eds. P. & L. Legendre. NATO ASI Series G14. Springer, Berlin, Germany.

RYAN B.F., JOINER B.L. & RYAN T.A. 1985. *MINITAB Handbook.* MINITAB, PWS-Kent, Boston.

SAKAI A.K. & ODEN N.L. 1983. Spatial pattern of sex expression in silver maple (*Acer saccharinum* L.): Morisita's index and spatial autocorrelation. *Amer. Nat.* 122: 489-508.

SARUKHAN J. 1978. Studies on the demography of tropical trees. In: *Tropical Trees as Living Systems.* Eds. Tomlinson P.B. & Zimmerman M.H. Cambridge University Press, London, UK.

SASAKI S. & MORI T. 1981. Growth responses of dipterocarp seedlings to light. *Malay. Forester* 44: 319-345.

SCHUPP E.W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology 71*: 504-515.

SCHUPP E.W. 1992. The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. *Am. Nat.* 140: 526-530.

SIMPSON E.H. 1949. Measurement of diversity. *Nature, London.* 163: 688.

SINCLAIR D.F. 1985. On tests of spatial randomness using mean nearest neighbour distance. *Ecology* 66: 1084-1085.

SINGH K.G. 1966. Ectotrophic mycorrhiza in equatorial rain forests. *Malay. Forester* 29: 13-18.

SORK V. 1987. Effects of predation and light on seedling establishment in *Gustavia superba. Ecology* 68: 1341-1350.

SPSS^X Inc. 1983. *SPSS^X User's Guide.* McGraw-Hill, New York, UK.

STERNER R.W., RIBIC C.A. & SCHATZ G.E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *J. Ecol.* 74: 621-633.

STRAUSS D.J. 1975. A model for clustering. *Biometrika* 62: 467-475.

STRENG D.R., GLITZENSTEIN J.S & HARCOMBE P.A. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecol. Monogr.* 59: 177-204.

STRONG D.R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree richness in the tropics without animals. *J. Biogeog.* 4: 215-218.

SWAINE M.D. 1989. Population dynamics of tree species in tropical forests. In *Tropical Forests. Botanical dynamics, speciation and diversity*. Eds. Holm-Nielson L.B., Nielson I.C. & Balslev H. Academic Press, London, UK.

SWAINE M.D. 1992. Population dynamics of moist tropical forest at Kade, Ghana In: *Actes de l'atelier sur l'aménagement de l'écosystème forestier tropical humide, Cayenne.* Eds. Maitre H.F. & Puig H. MAB/UNESCO/IUFRO/FAO.

SWAINE M.D. & HALL J.B. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. *J. Trop. Ecol.* 4: 253-269.

SWAINE M.D. & LIEBERMAN D. 1987. Note on the calculation of mortality rates. *J. Trop. Ecol.* 3: ii-iii.

SWAINE M.D., PUTZ F.E. & LIEBERMAN D. 1987. The dynamics of tree populations in tropical forest: a review. *J. Trop. Ecol.* 3: 359-366.

SWAINE M.D. & WHITMORE T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.

SZWAGRZYK J. 1990. Natural regeneration of forest related to the spatial structure of trees: A study of two forest communities in Western Carpathians, southern Poland. *Vegetatio* 89: 11-22.

THORINGTON R.W., TANNENBAUM B., TARAK A. & RUDRAN R. 1982. Distribution of trees on Barro Colorado Island: Five hectare sample. In: *The Ecology of a Tropical Forest: Seasonal rhythms and long-term changes.* Eds. Leigh E.G., Rand A.S. & Windsor D.M. Smithsonian Institute Press, Washington, D.C., USA.

TILMAN D. 1982. *Resource Competition and Community Structure.* Princeton University Press, New Jersey, USA.

TURNER I.M. 1990. The seedling survivorship and growth of three *Shorea* species in a Malaysian tropical rain forest. *J. Trop. Ecol.* 6: 469-478.

UHL C. 1982. Tree dynamics in a species rich tierra firme forest in Amazonia, Venezuela. *Acta Cientifica Venezolana* 33: 72-77.

UPTON G.J.G. & FINGLETON B. 1985. *Spatial Data Analysis by Example.* Wiley, New York, USA.

VANDERMEER J. 1977. Notes on density dependence of *Welfia,* a lowland rain forest species in Costa Rica. *Brenesia* 10/11: 9-15.

WALLACE A.R. 1878. *Tropical Nature and Other Essays.* Macmillan, London, UK.

WALSH R.P.D. 1990. *Climatic data for Danum Valley.* Unpublished Danum Valley Field Centre Report No. 98. Sabah, Malaysia.

WALTON A.B. 1936. Experimental treatment plots. *Malay. Forester* 5: 53-57.

WARNER R.R & CHESSON P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125: 769-787.

WEBB L.J., TRACEY J.G. & WILLIAMS W.T. 1972. Regeneration and pattern in the subtropical rain forest. *J. Ecol.* 60: 675-695.

WEBBER M.L. 1934. Fruit dispersal. *Malay. Forester* 3: 18-19.

WELDEN C.W., HEWETT, S.W., HUBBELL S.P. & FOSTER R.B. 1991. Sapling survival, growth and recruitment: relationship to canopy height in a neo-tropical forest. *Ecology* 72: 35-50.

WHITMORE T.C. 1982. On pattern and process in forests. *J. Ecol.* 70: 45-59.

WHITMORE T.C. 1984. *Tropical Rain Forests of the Far East.* Second Edition. Oxford University Press, Oxford, UK.

WHITMORE T.C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70: 536-538.

WIENS J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

WILLIAMSON G.B. 1975. Pattern and seral composition in an old-growth beech-maple forest. *Ecology* 56: 727-731.

WONG F.O. 1973. A study of the growth of the main commercial species in Segaluid-lokan Forest Reserve, Sandakan, Sabah. *Malay. Forester* 36: 20-37.

WOODS P. 1985. Drought and fire in tropical forests in Sabah - an analysis of rainfall patterns and some ecological effects. *3rd International Round Table Conference on Dipterocarps,* Samarinda, Indonesia.

WRIGHT P.S. 1975. *The soils of Sabah.* Vol 3, western parts of Tawau and Lahad Datu Districts. Land Resource Study 10. Ministry of Overseas Development, London, UK.

WRIGHT S.J. & HOWE H.F. 1987. Pattern and mortality in Colorado Desert plants. *Oecologia* 73: 543-552.

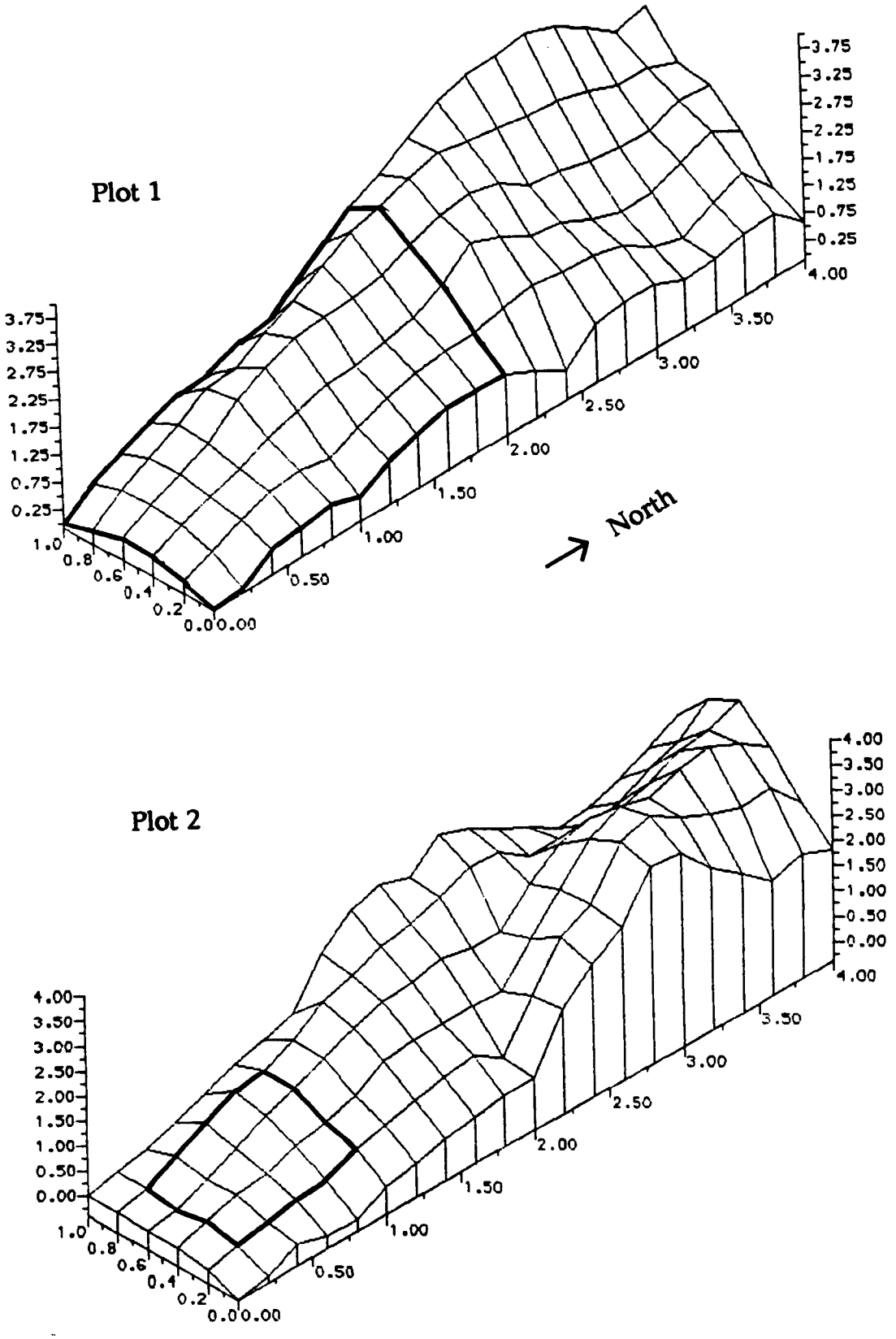
WYATT-SMITH J. 1958. Seedling/sapling survival of *Shorea leprosula, Shorea parvifolia* and *Koompassia malaccensis*. *Malay. Forester* 21: 185-193.

WYATT-SMITH J. 1966a. Ecological studies on Malayan forests. *Malayan Forestry Department Research Pamphlet 52*. Forest Research Institute, Kepong, Malaysia.

WYATT-SMITH J. 1966b. Manual of Malayan silviculture for inland forests. *Malayan Forestry Record 23*. Forest Research Institute, Kepong, Malaysia.

WYATT-SMITH J. 1987. Foreword to: The dynamics of tree populations in tropical forest. Eds. Swaine M.D. & Lieberman D. *J. Trop. Ecol.* 3: iv.

ZAR J.H. 1984. *Biostatistical Analysis*. Second Edition. Prentice-Hall International, Englewood Cliffs, New Jersey, USA.



Appendix 1 Diagram of the topography of Plot 1 (above) and Plot 2, showing the location of the seedling study areas (outlined in bold). Plot 1 seedling study area was 2 ha; Plot 2, 0.48 ha. Horizontal scale is m x 10^2; vertical scale is m x 10 above the south-east corner.

Appendix 2 List of Dipterocarpaceae present in Plots 1 and 2. Nomenclature follows Ashton (1982). [Abbreviated names used in tables and figures for species present in seedling study areas are given in brackets].

Dipterocarpus verrucosus FOXW. ex SLOOT
D. caudiferus MERR.
D. kerrii KING

Anisoptera costata KORTH.

Parashorea malaanonan (BLCO) MERR. **[P mala]**

Hopea nervosa KING **[H nerv]**

Section *Shorea* (selangan batu)
Shorea seminis (DE VRIESE) SLOOT.
S. atrinervosa SYM.
S. falciferoides ssp. *glaucescens* (MEIJER) ASHTON
S. superba SYM.

Section *Richetioides* (Yellow Meranti)
S. angustifolia ASHTON

Section *Anthoshorea* (White Meranti)
S. symingtonii WOOD **[S symi]**
S. agamii ASHTON **[S agam]**

Section *Brachypterae* (Red and Dark Red Meranti) **[DRM]**
S. parvistipulata HEIM
S. pauciflora KING **[S pauc]**
S. johorensis FOXW. **[S joho]**
S. fallax MEIJER **[S fall]**

Section *Pachycarpae* (Red Meranti)
S. pilosa ASHTON **[S pilo]**
S. mecistopteryx RIDL.

Section *Mutica* (Light Red Meranti) **[LRM]**
S. argentifolia SYM. **[S arge]**
S. leprosula MIQ. **[S lepr]**
S. parvifolia DYER **[S parv]**

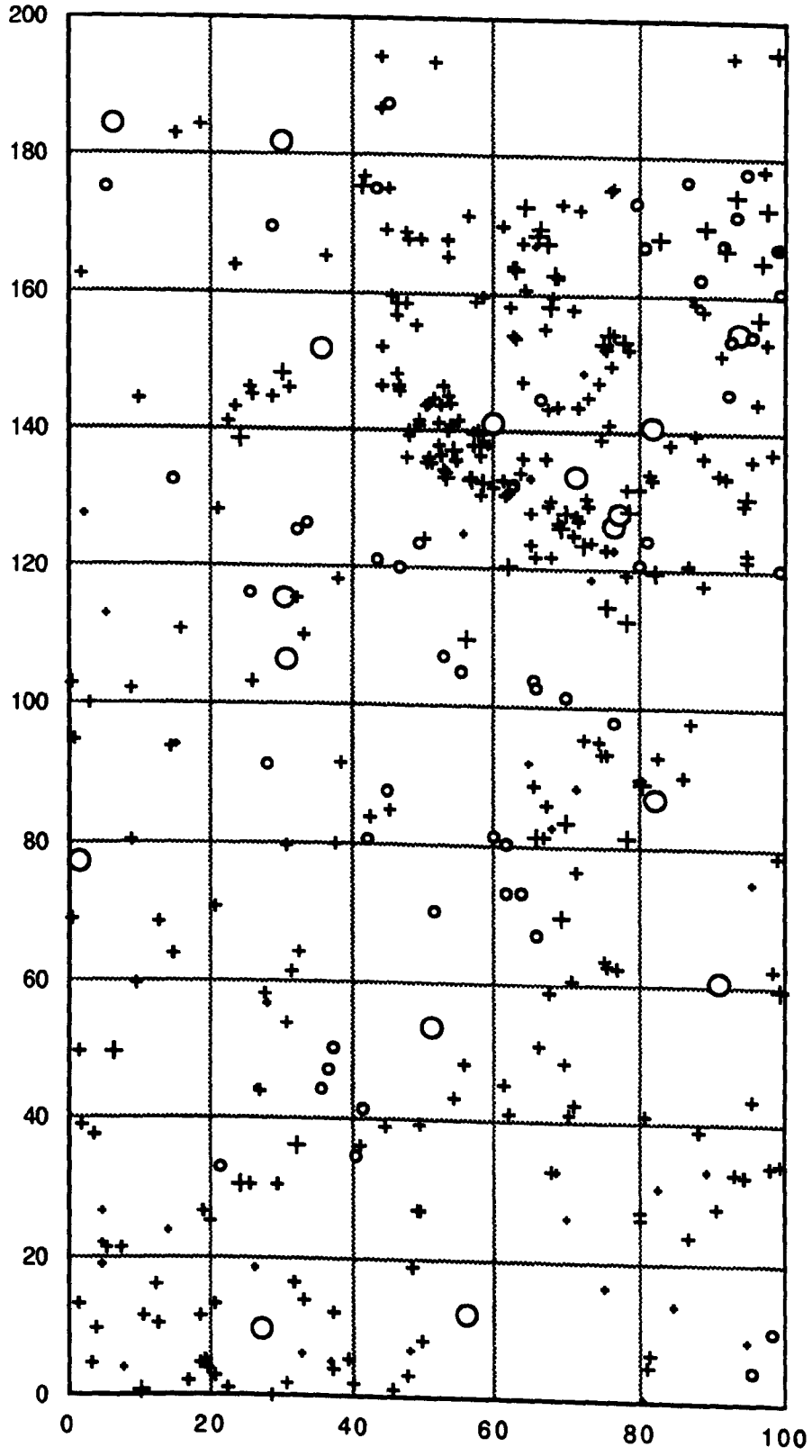
Vatica umbonata (HOOK. f.) BURCK
V. sarawakensis HEIM **[V sara]**
V. albiramis SLOOT
V. oblongifolia HOOK. f.
V. dulitensis SYM. **[V duli]**
V. vinosa ASHTON

Appendix 3 Maps of the spatial distributions of dipterocarp seedlings and trees in the seedling study areas of the main plots. Maps are oriented with north at the top, and scale is in metres.

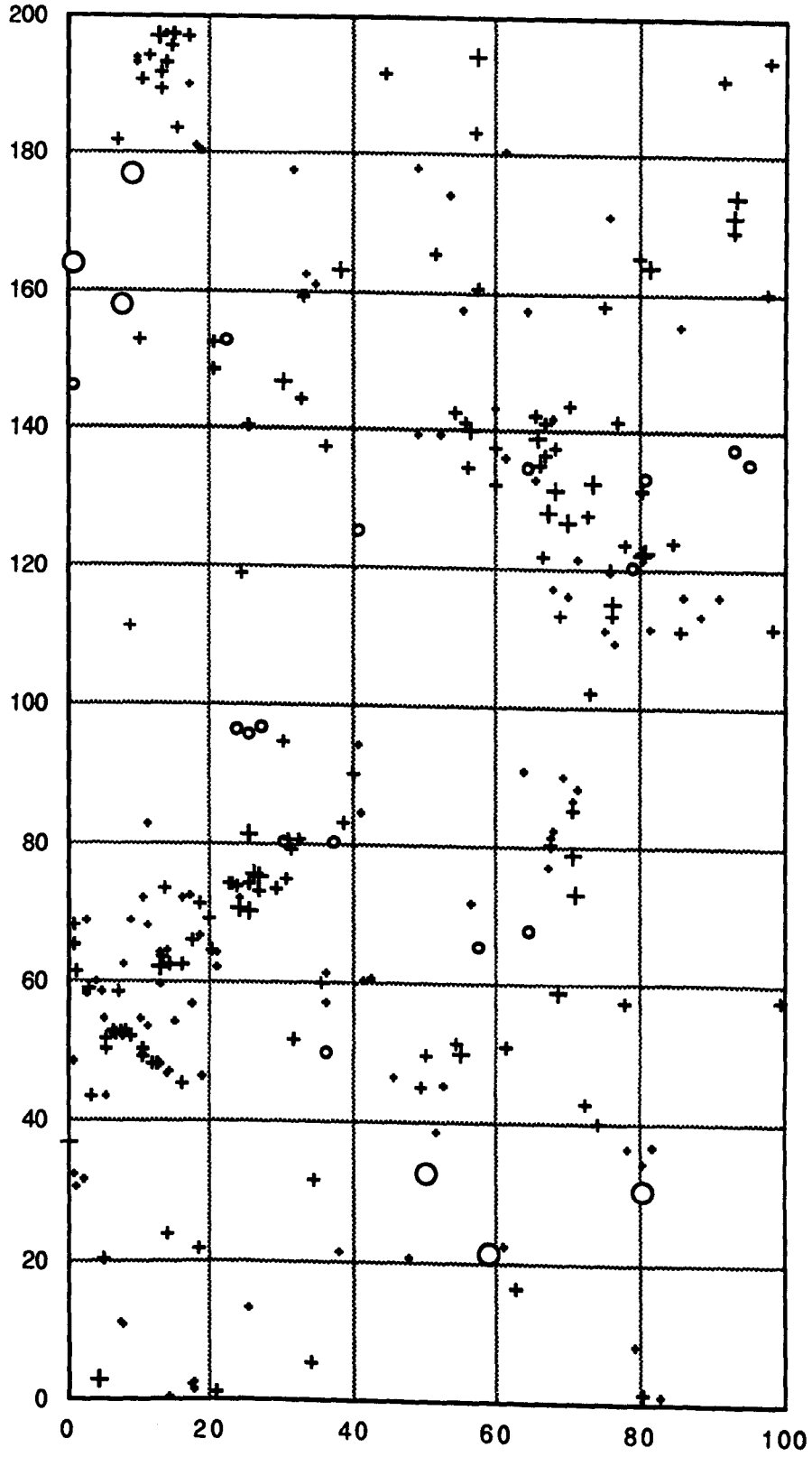
A. Plot 1 (2 ha).

KEY

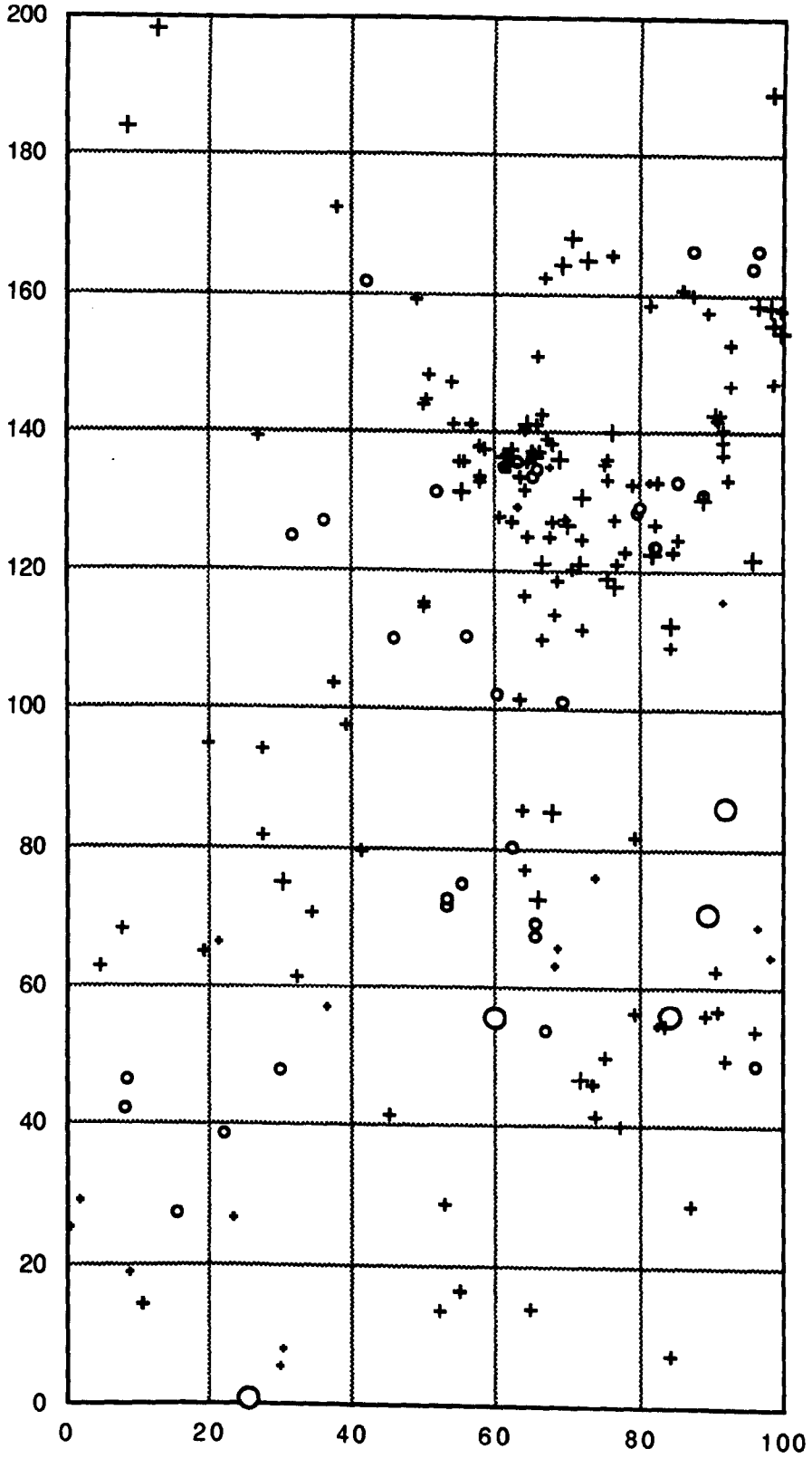
O	Trees >100 cm gbh
o	Trees 10.0 cm gbh - 99.9 cm gbh
+	Seedlings >250 cm tall
+	Seedlings 51-250 cm tall
•	Seedlings <50 cm tall



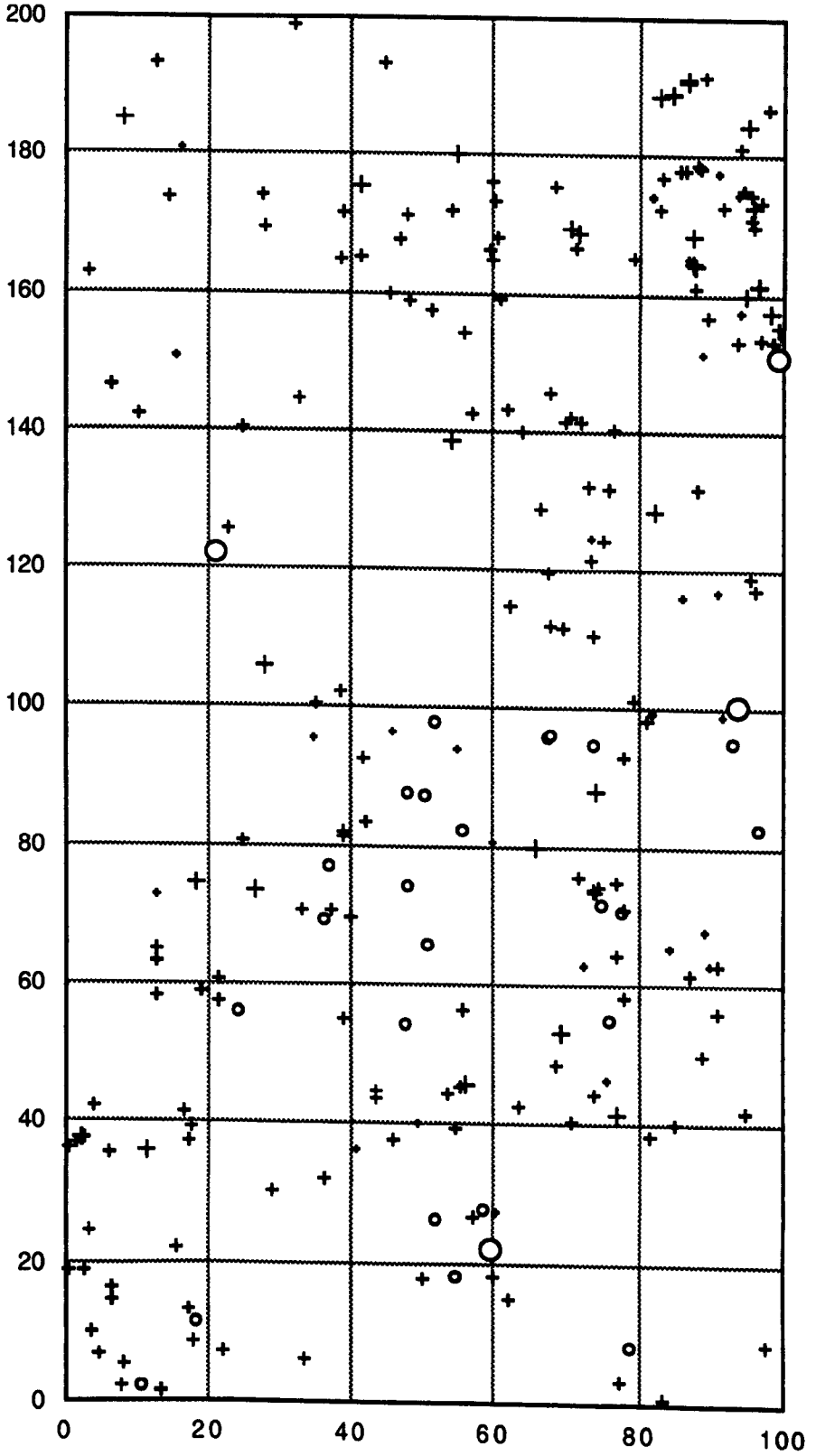
Shorea johorensis



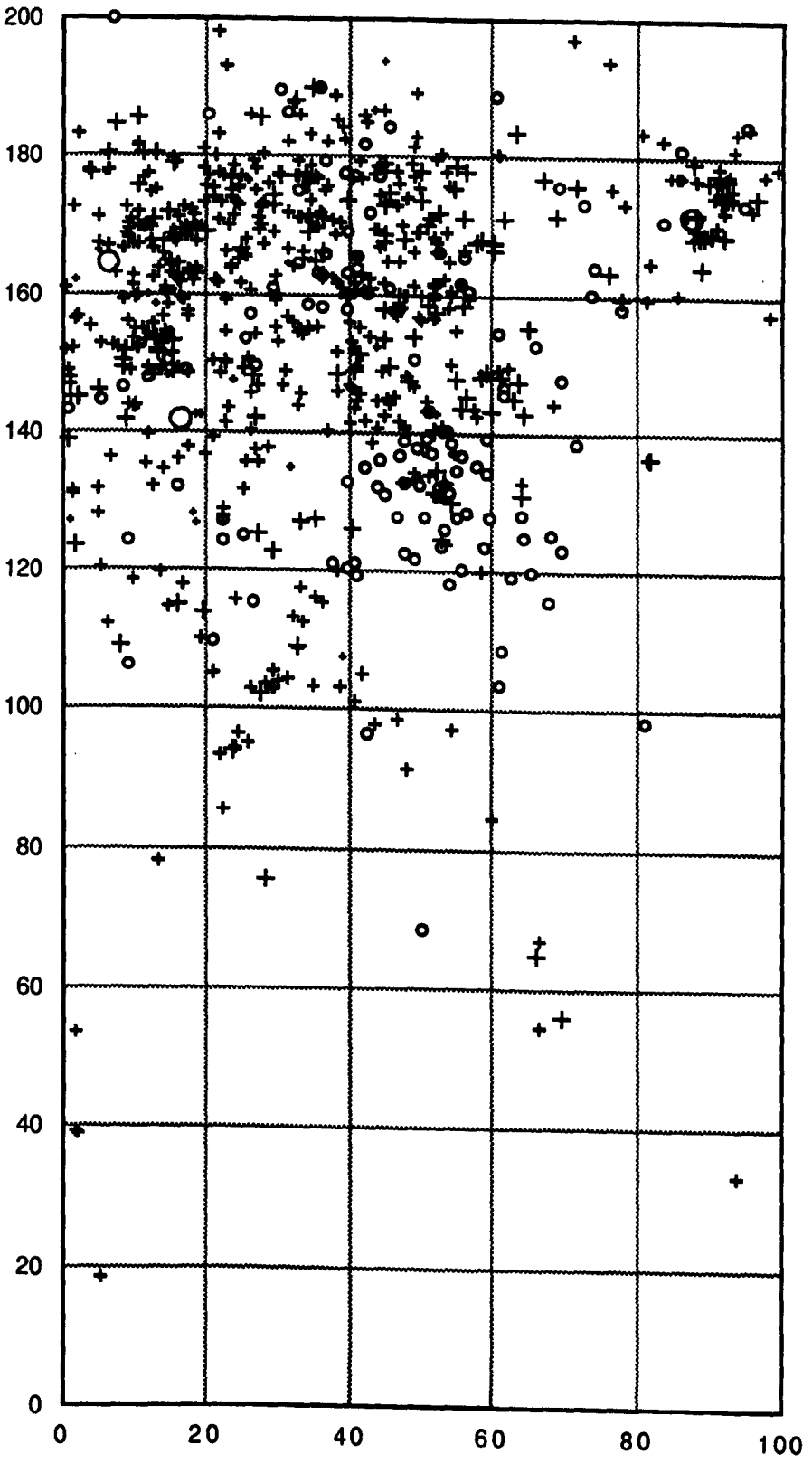
Shorea argentifolia



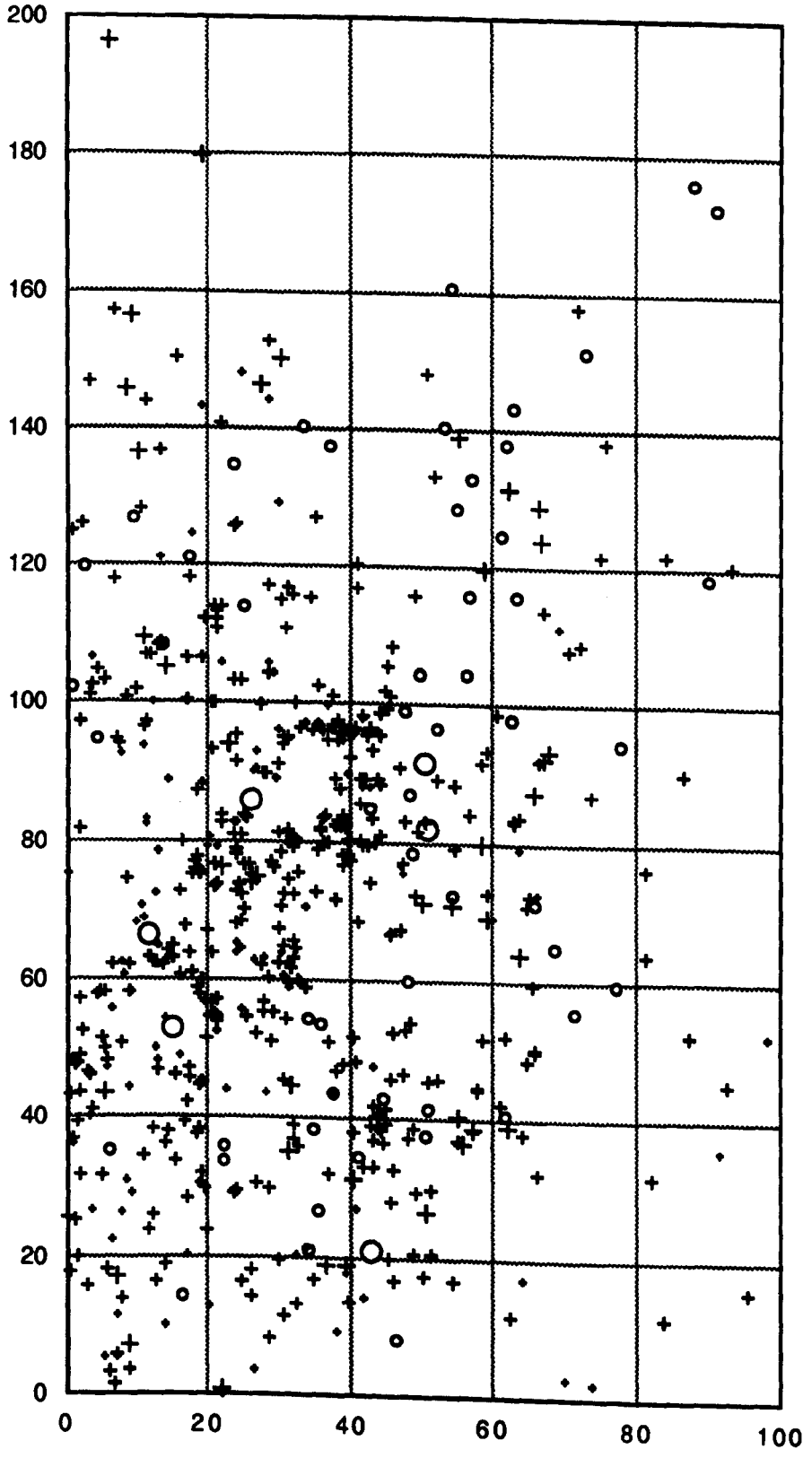
Shorea leprosula



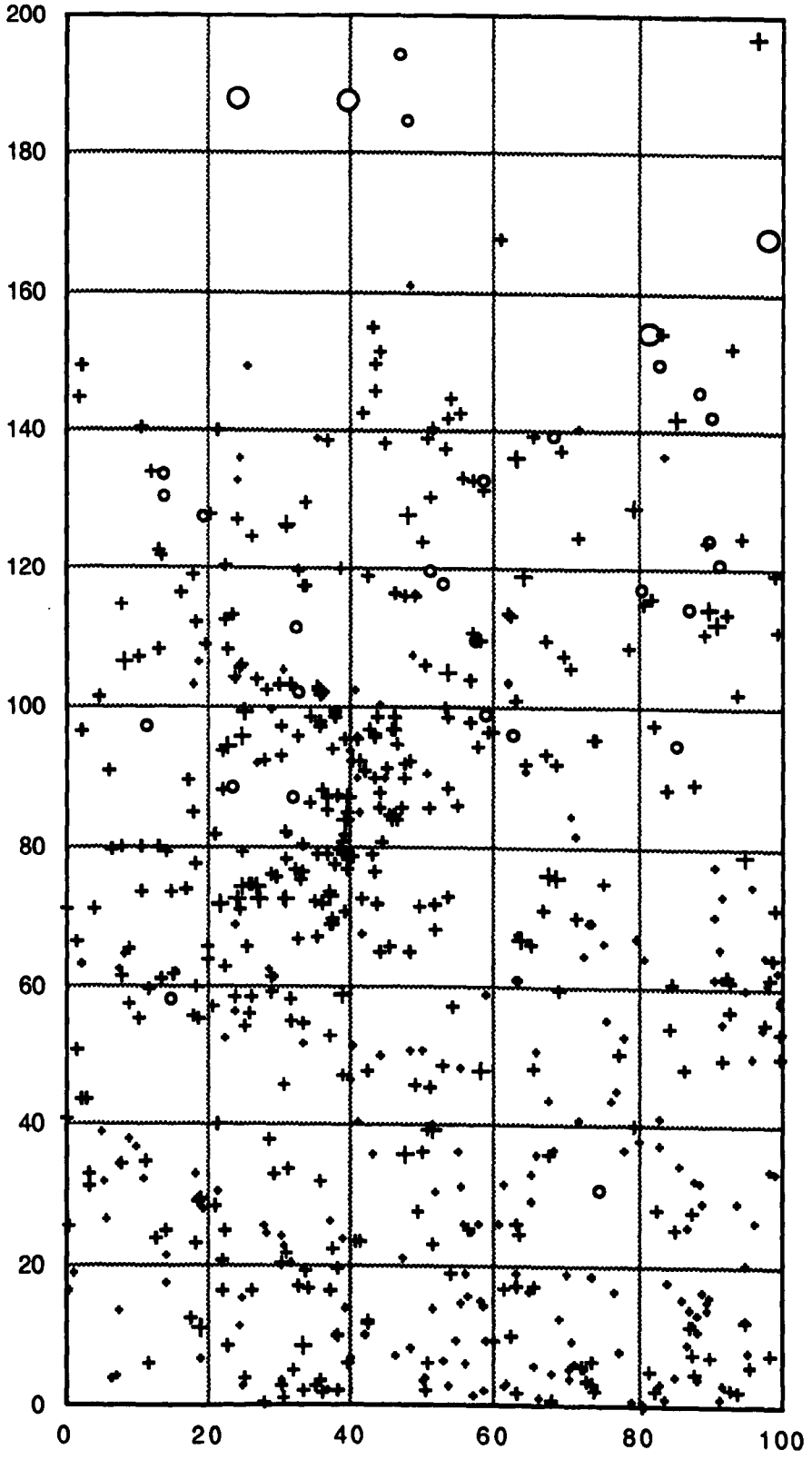
Shorea parvifolia



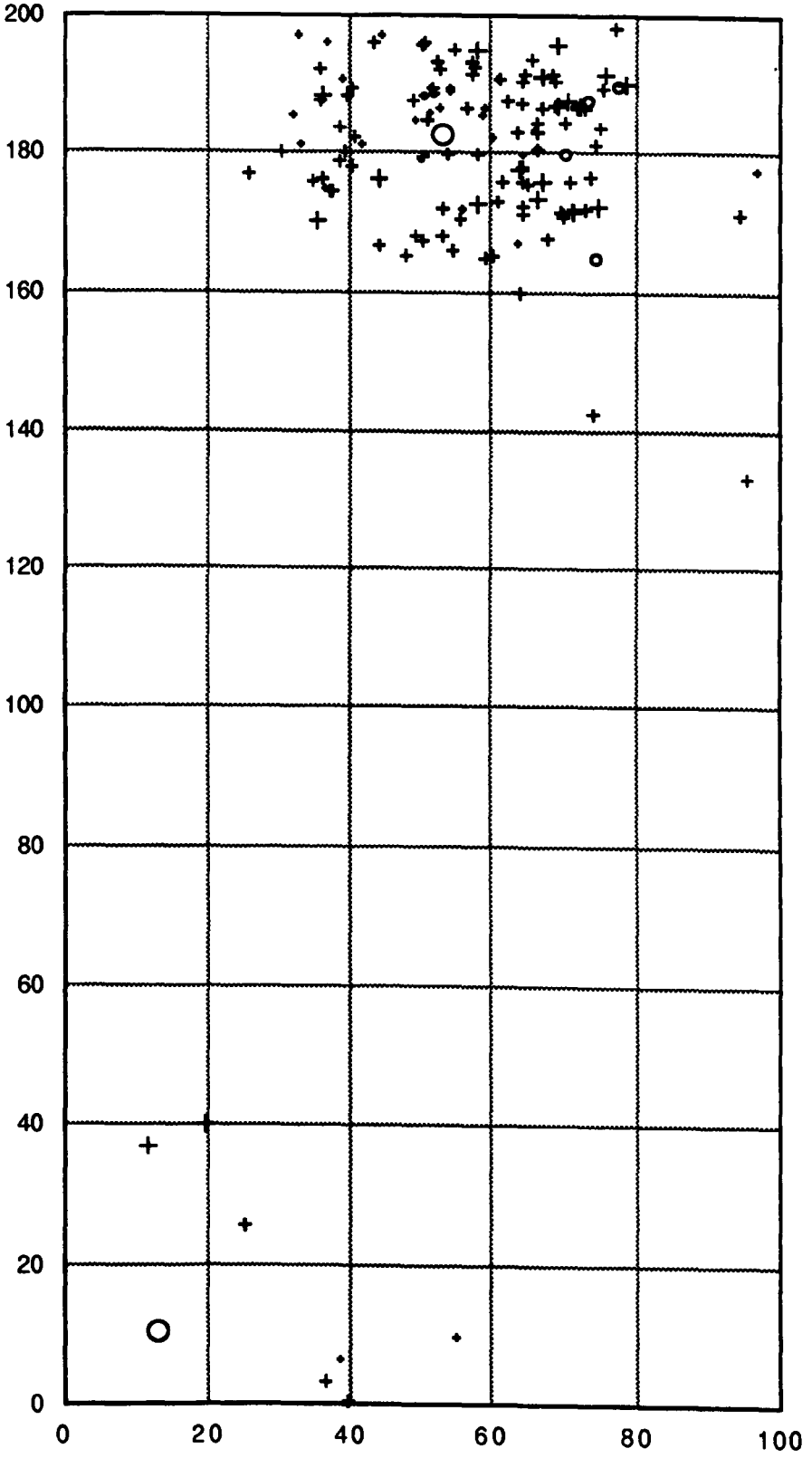
Shorea fallax



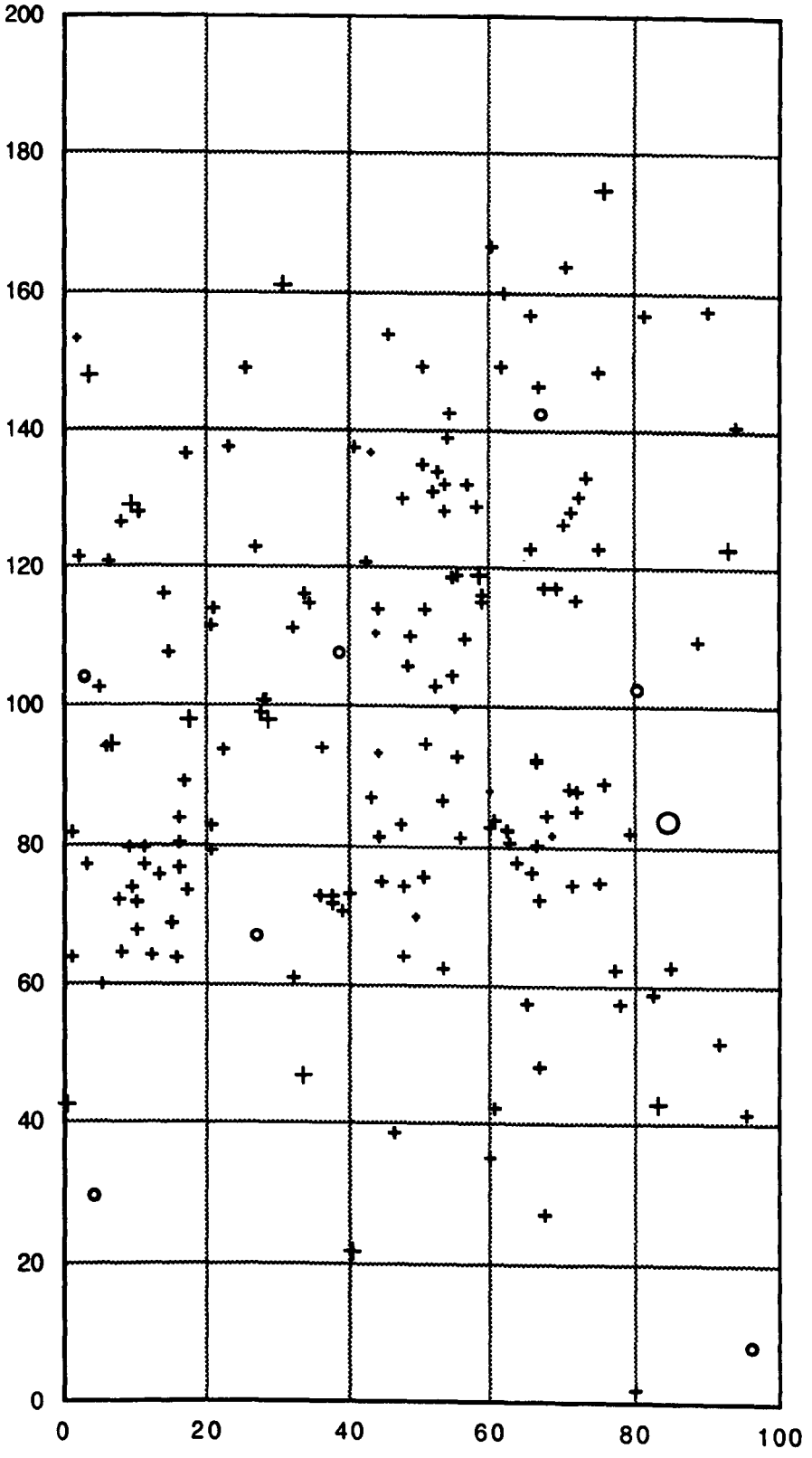
Shorea pauciflora



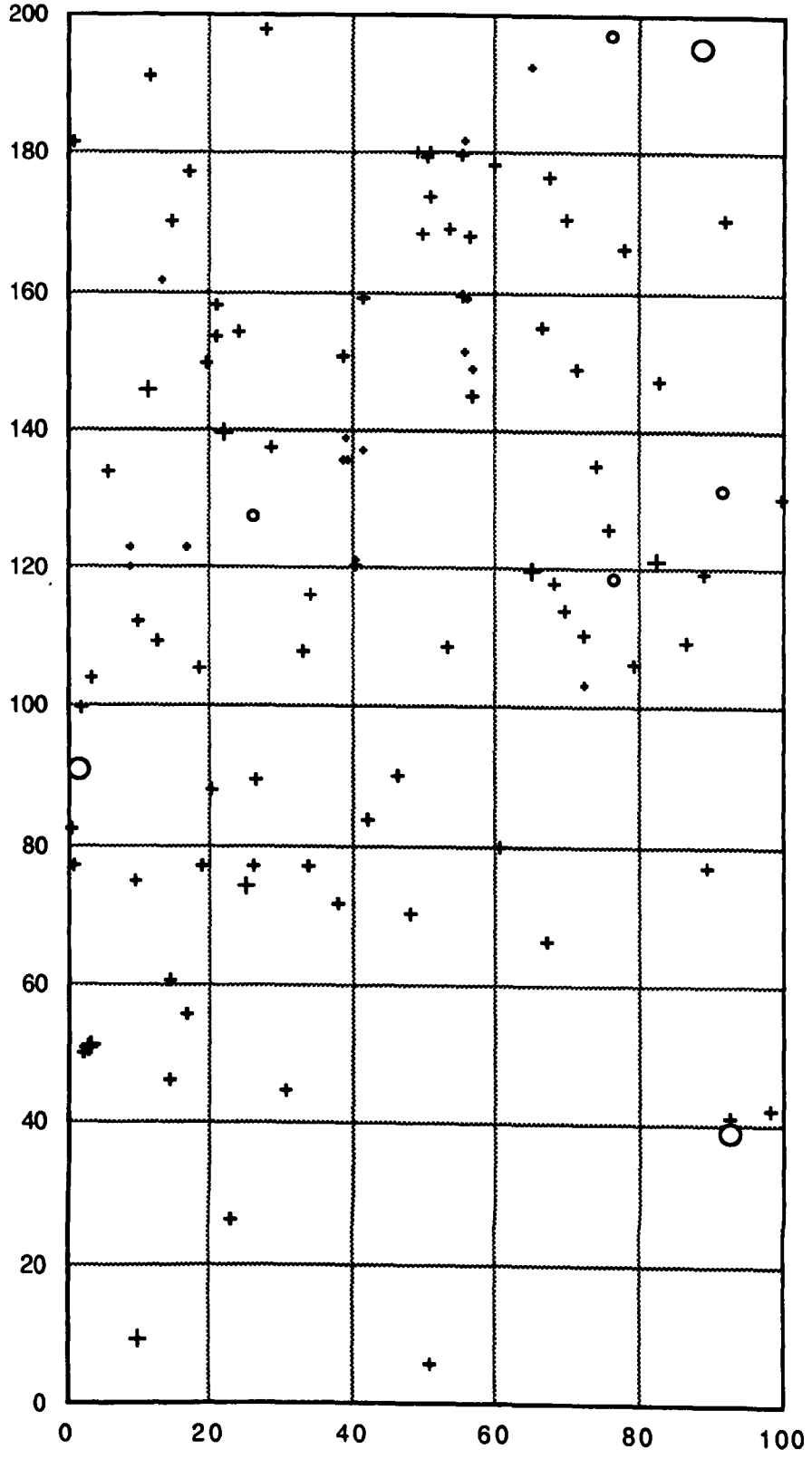
Parashorea malaanonan



Hopea nervosa



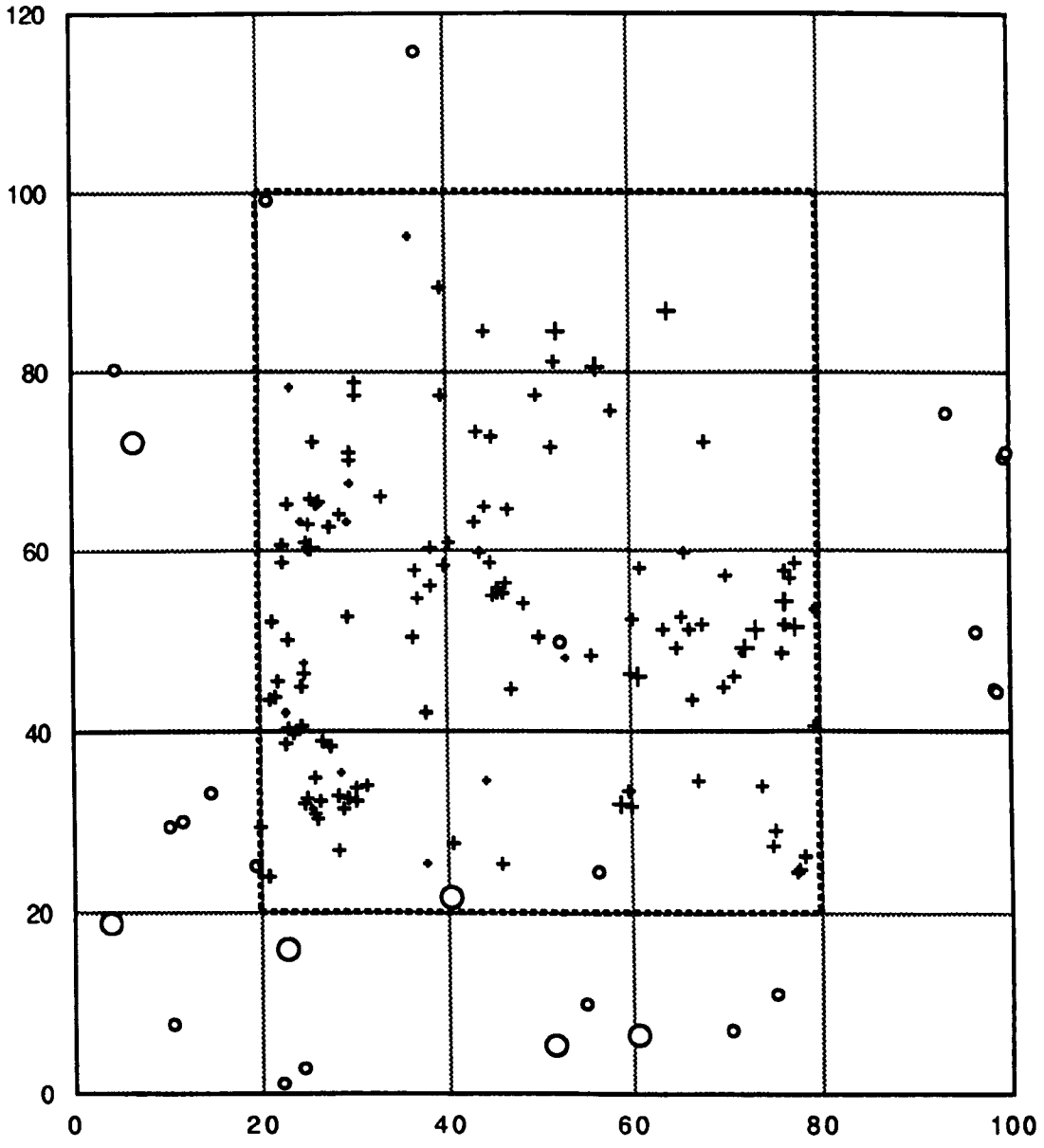
Shorea agamii



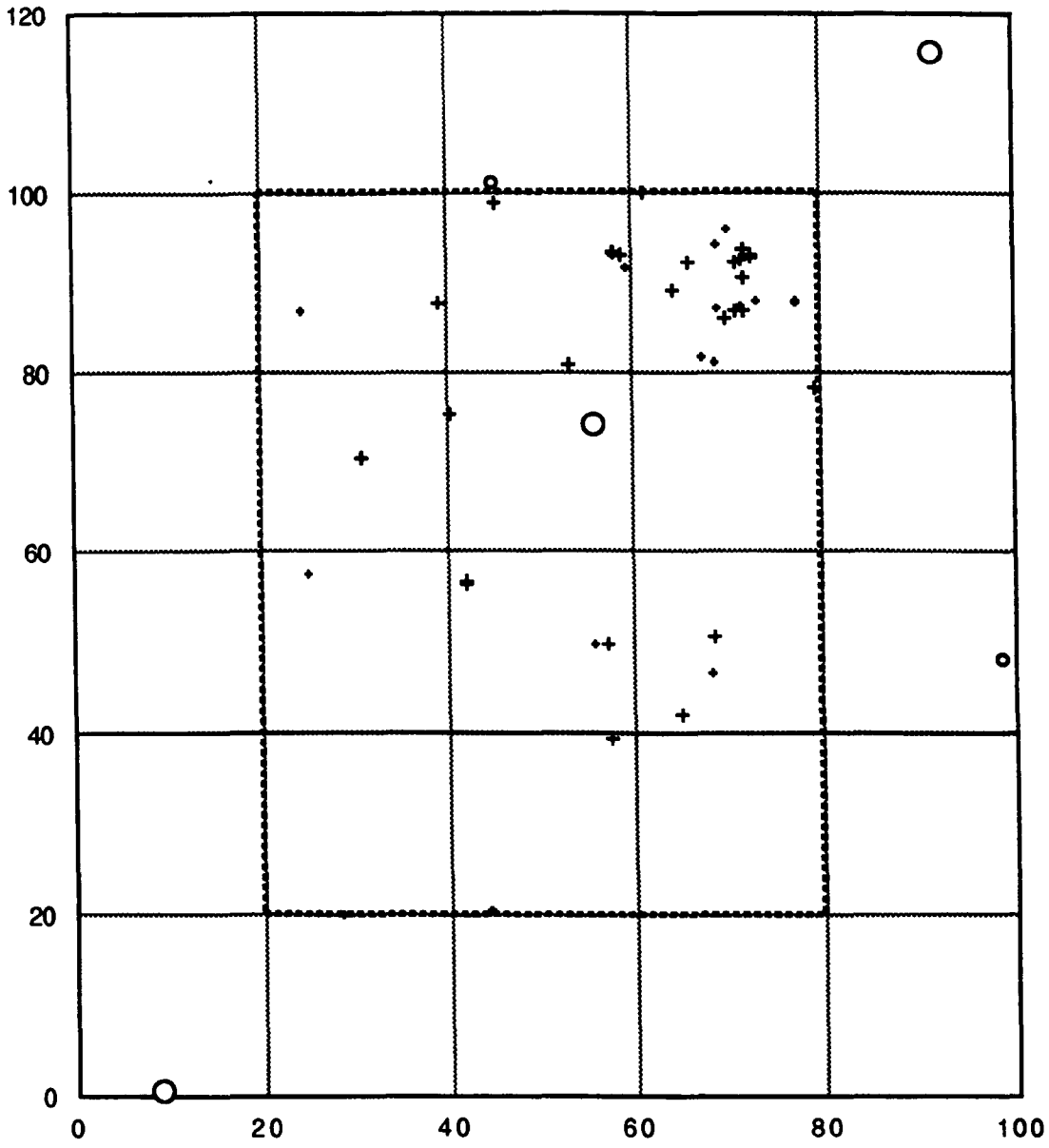
Vatica sarawakensis

Appendix 3 **B. Plot 2 (0.48 ha).**

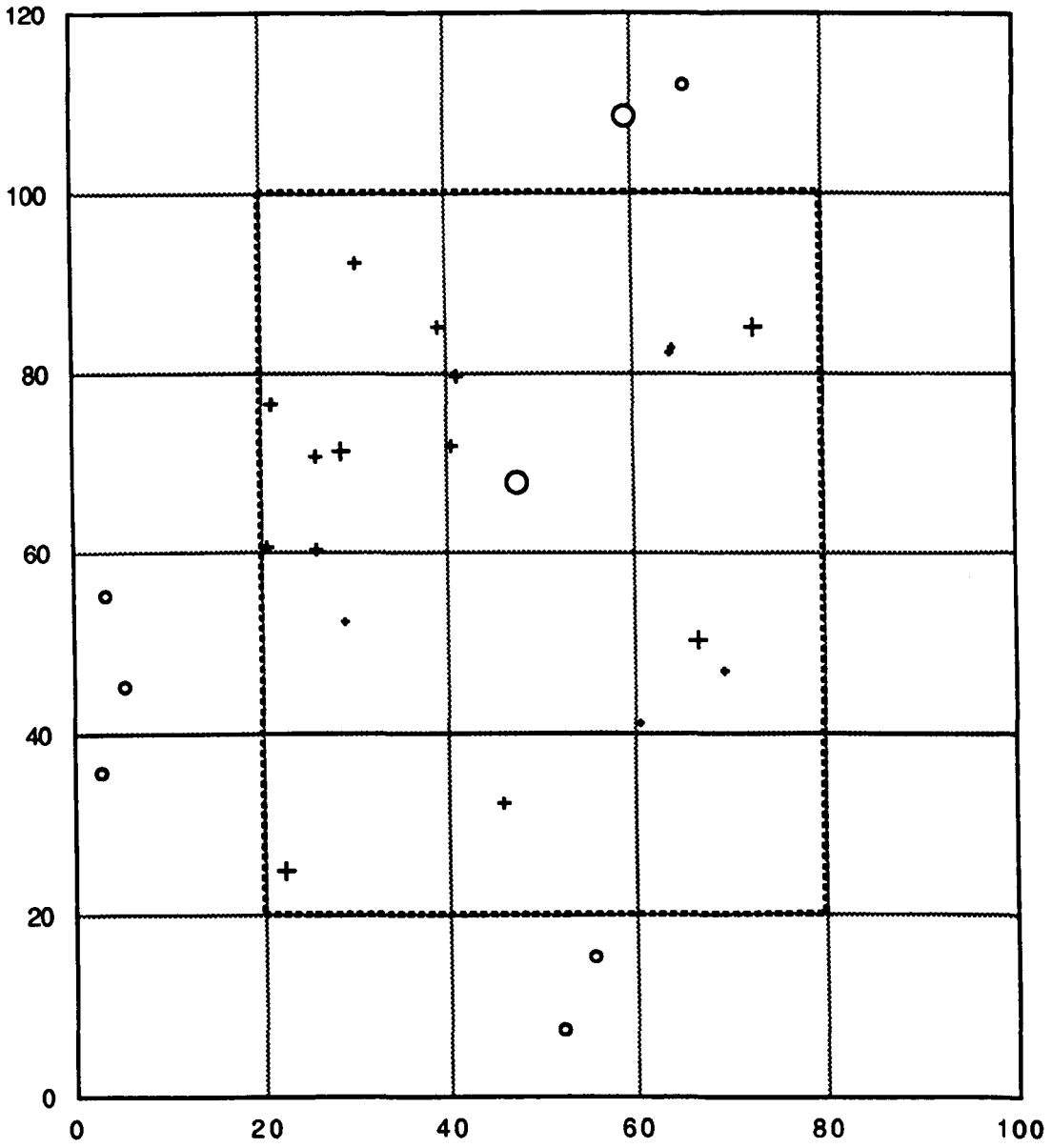
The southern 1.2 ha area of Plot 2 is shown, with the seedling study area outlined by dashed lines.



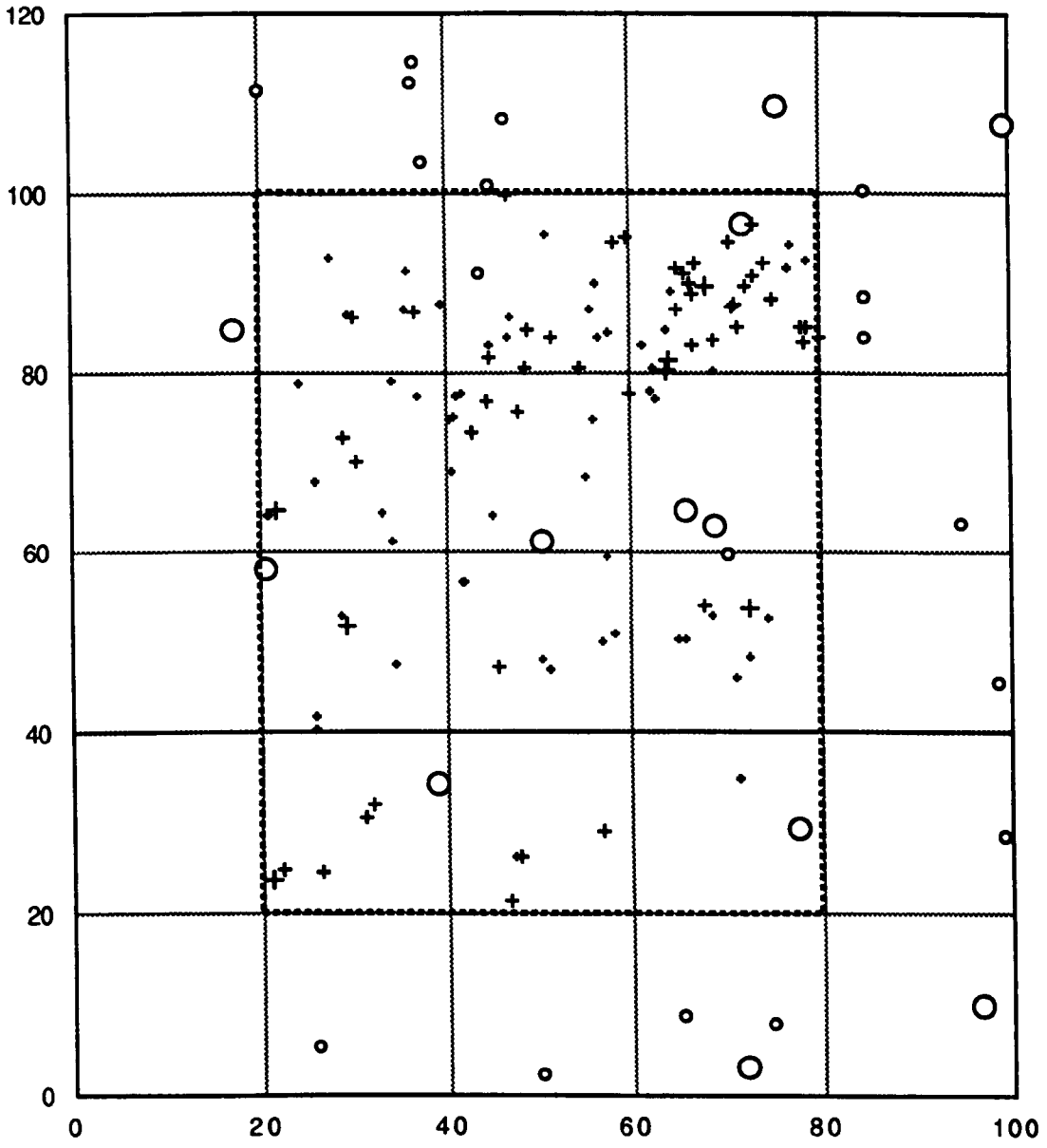
Shorea johorensis



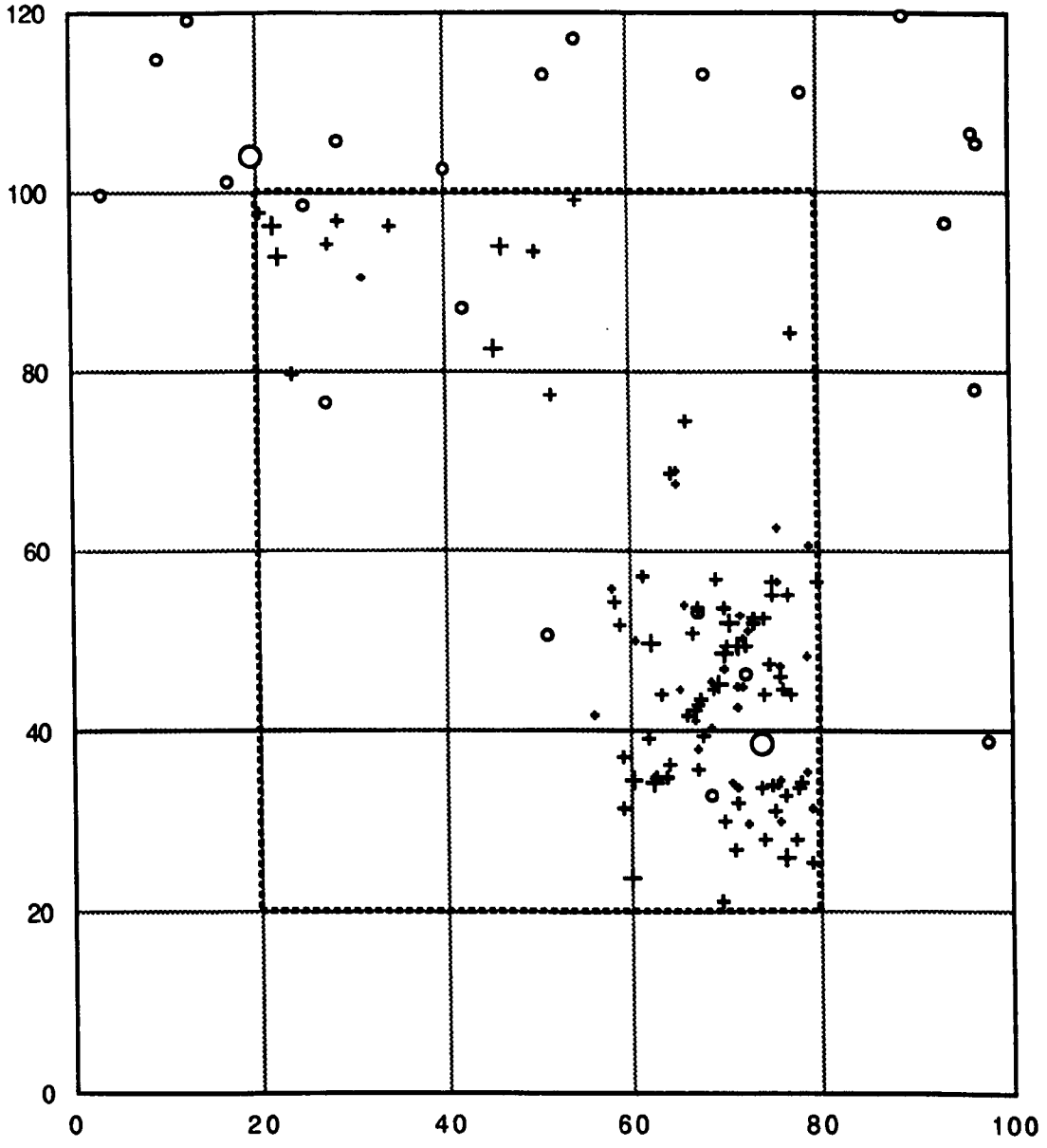
Shorea argentifolia



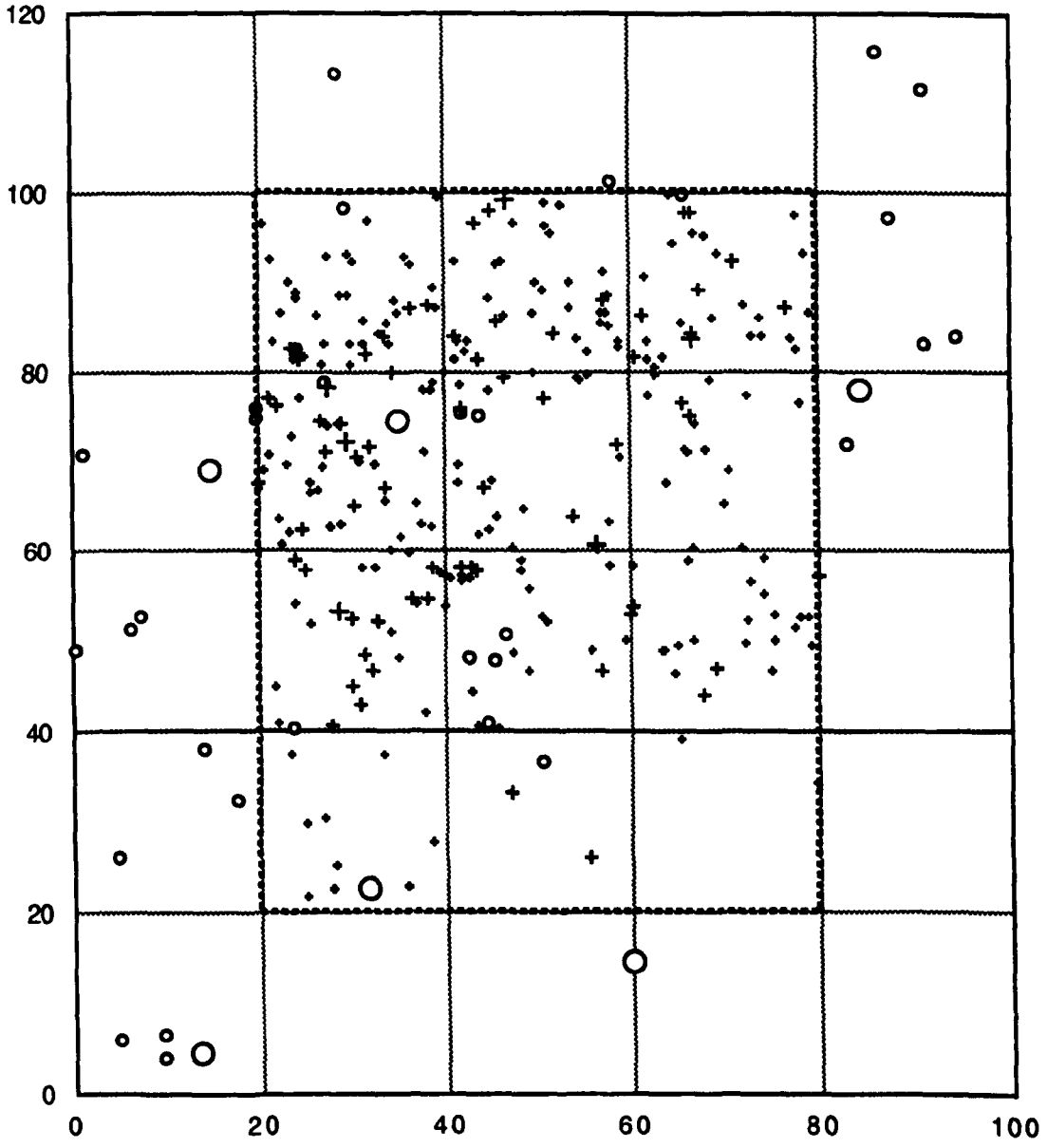
Shorea leprosula



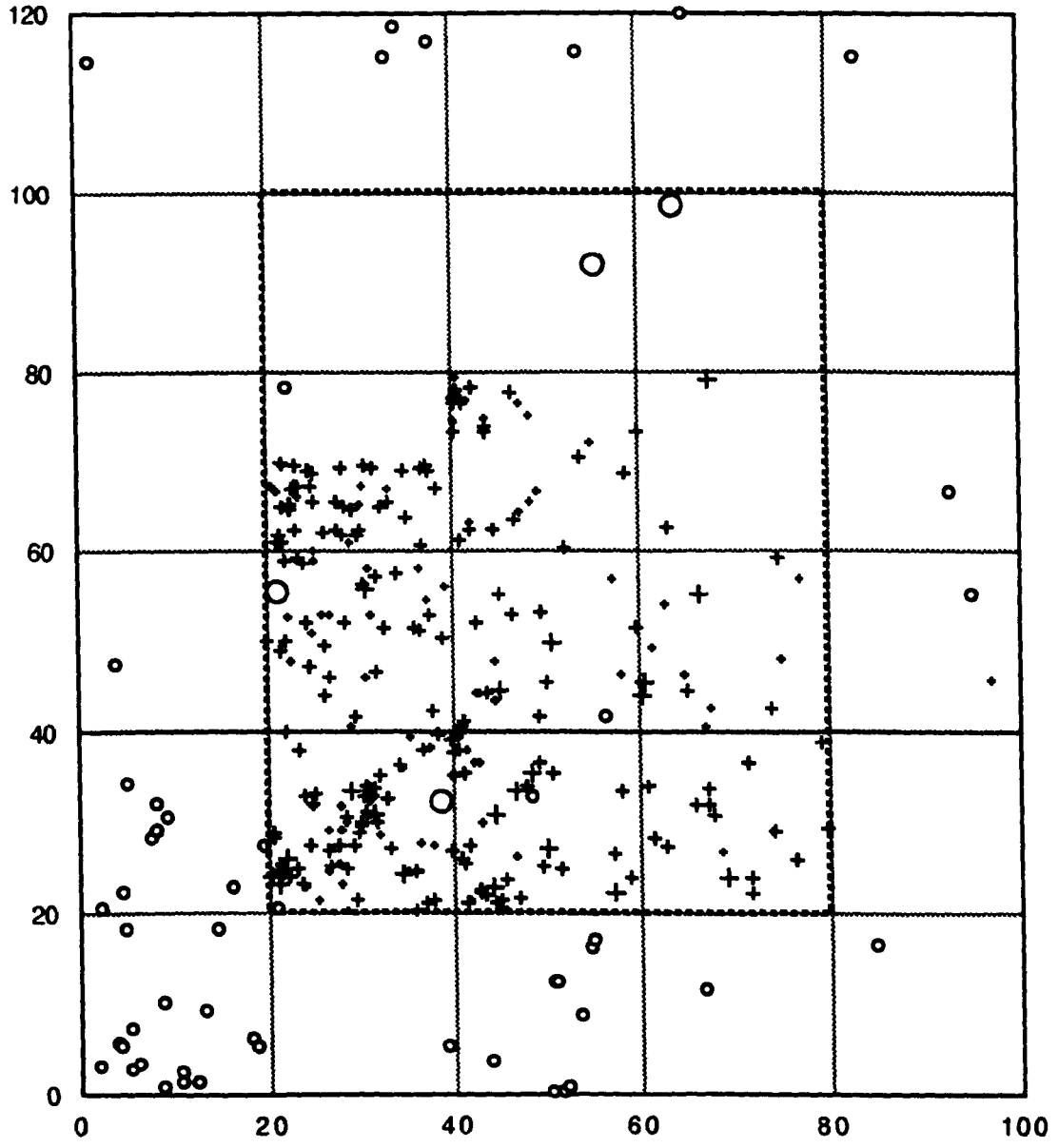
Shorea parvifolia



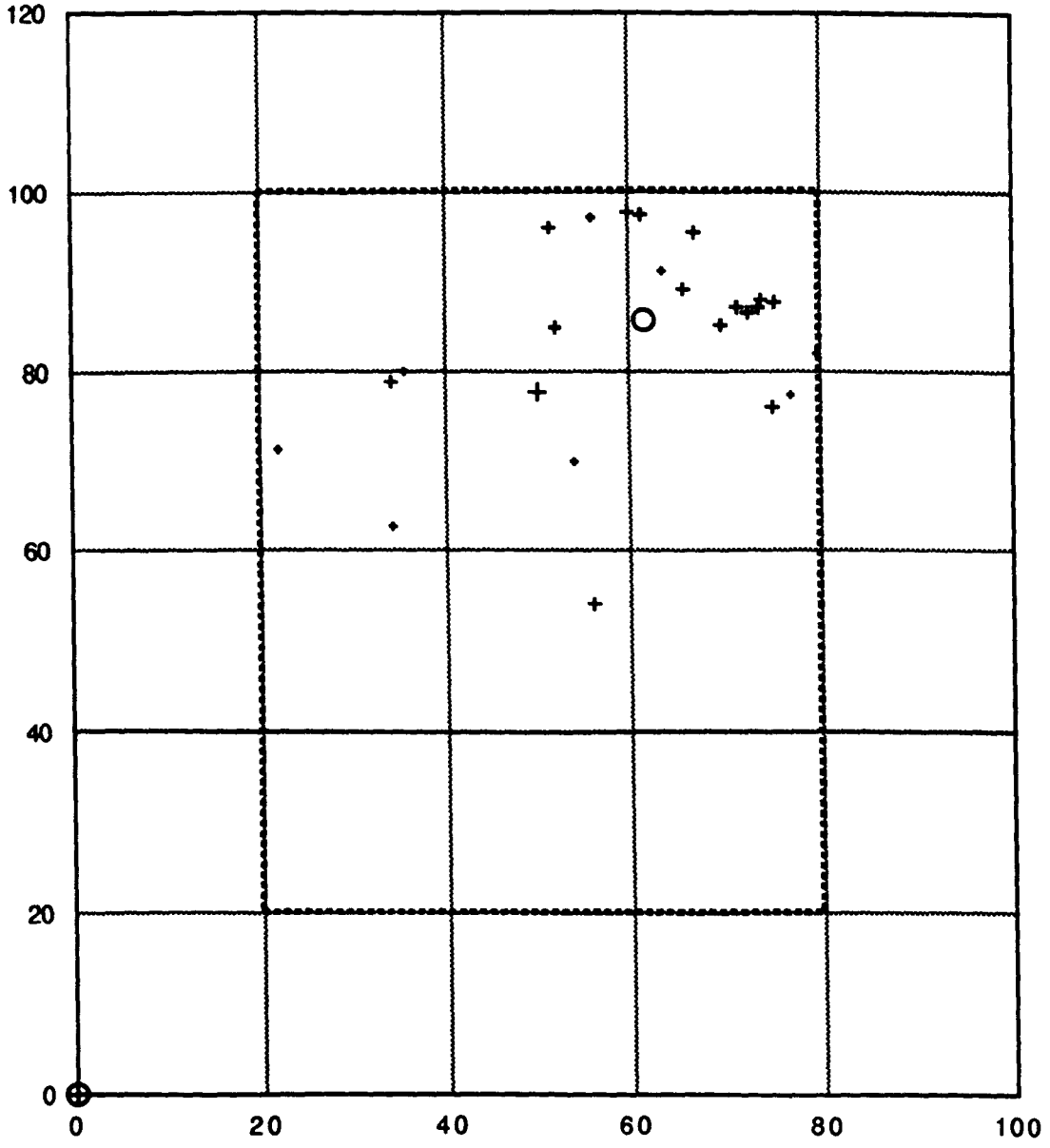
Shorea fallax



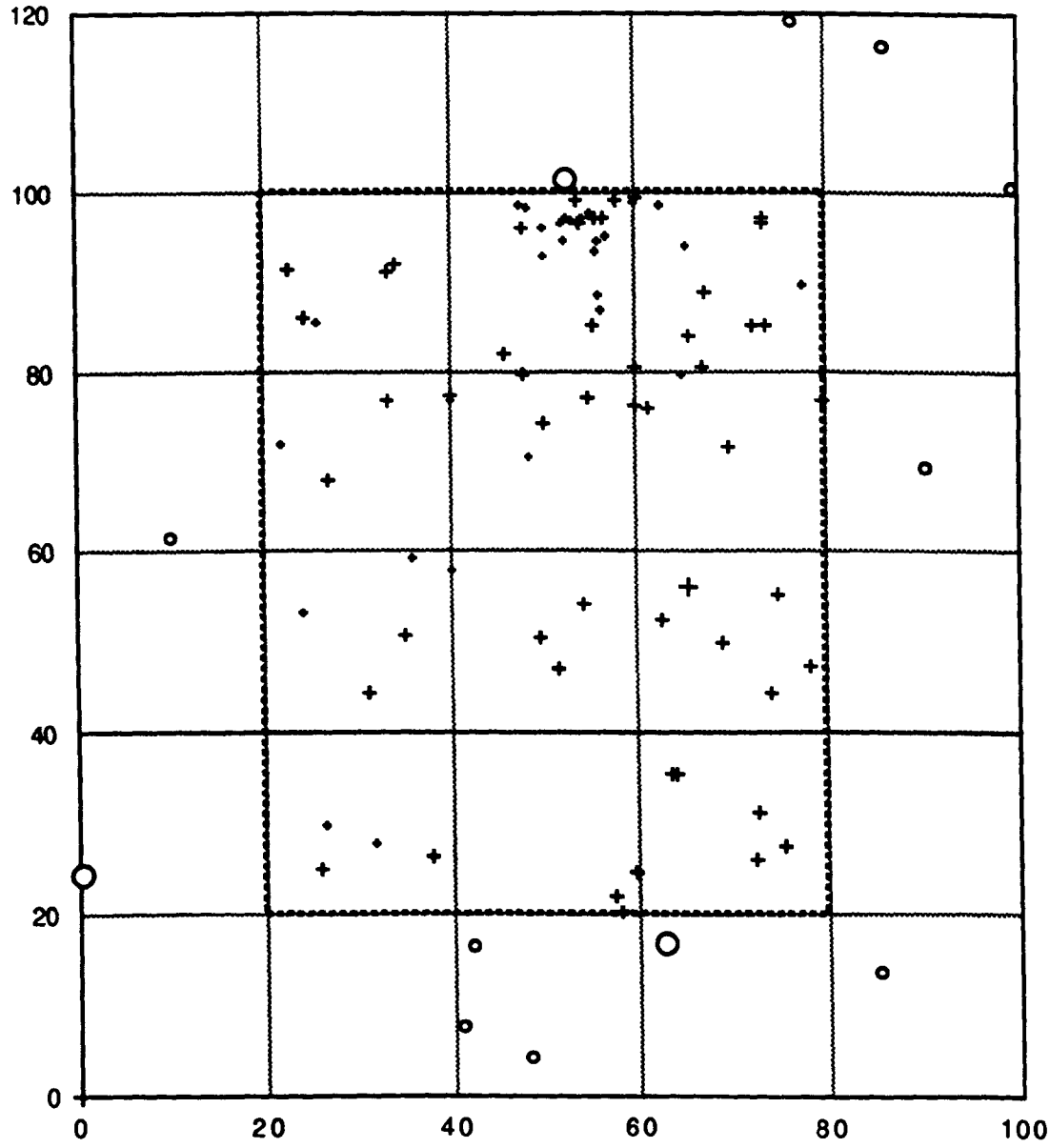
Parashorea malaanonan



Hopea nervosa



Shorea pilosa



Vatica sarawakensis

Appendix 4 Numbers of seedlings enumerated week-by-week in the first enumeration of Plot 1, and median and mean dates of enumeration for each species.

Species	Week of enumeration (week 0 = 20/7/86)							Total seedlings	Median week	Mean week
	0	3	5	6	7	8	9			
S joho	100		41	82	68	7	2	300	6	4.2
S arge	112	1	15	32	20	24	4	208	0	2.9
S lepr	43		19	56	27	3		148	6	4.4
S parv	78	3	12	17	60	16	1	187	5.5	3.9
S fall	15	4	28	154	165	198		564	7	6.8
S pauc	362	31	51	38	3	2	5	492	0	1.3
P mala	378	43	51	60	7	1	1	541	0	1.5
H nerv	7				40	71		118	8	7.2
S agam	57	8	23	44	13	1		146	5	3.4
S sp10	10		2	3	4			19	0	2.9
S symi	1		2	2				5	5	4.4
V duli	6	49	28	104			661	848	9	8.1
V sara	10	1	11	24	20	7		73	6	5.4
Unknown	7	1				2		10	-	-
Total	1186	141	283	616	427	332	674	3659		

Appendix 5 Area (cumulative percent) of the plot in 5m distance regions from different species of focal adult tree in Plot 1. Areas were calculated from a grid of points, considering each focal adult species separately.

Species	Number of adults	Distance region (m)						
		> 0 - 5	5 - 10	10 - 15	15 - 20	20 - 25	25 - 30	> 30
S joho	17	6.2	21.8	42.7	63.7	79.9	90.4	100
S arge	6	2.2	7.5	13.8	20.8	27.8	34.3	100
S lepr	5	1.8	6.7	12.2	17.9	24.1	30.7	100
S parv	4	1.4	5.4	11.6	20.2	30.6	41.4	100
S fall	3	1.2	4.5	9.3	14.2	19.7	25.8	100
S pauc	6	2.4	8.5	16.6	24.9	33.0	40.1	100
P mala	4	1.5	5.5	10.5	15.6	21.3	26.5	100
H nerv	2	0.8	3.1	6.6	10.5	14.8	19.6	100
S agam	1	0.4	1.6	3.5	5.8	8.5	11.4	100
V duli	1	0.4	1.6	3.5	6.3	9.8	14.1	100
V sara	3	1.1	3.6	7.0	11.3	16.6	22.8	100

Appendix 6 Observed (O) and Expected (E) numbers of seedlings in 5 m distance regions from different species of focal adult in Plot 1, and χ^2 value from a goodness-of-fit test (in brackets). Because tests within each species are not independent, P=0.007 was used. Bold figures indicate significant departure from expected value at P<0.007 (χ^2 =7.24).

	Distance region (m)						
	> 0 - 5	5 - 10	10 - 15	15 - 20	20 - 25	25 - 30	> 30
Species	O E	O E	O E	O E	O E	O E	
S joho	25 20.7 (0.89)	**88** 52.0 (24.83)	73 69.5 (0.17)	56 53.9 (2.72)	42 53.9 (2.64)	38 35.2 (0.23)	**11** 31.8 (13.64)
S arge	2 5.4 (2.10)	7 13.0 (2.79)	11 15.3 (1.22)	16 17.2 (0.08)	7 17.2 (6.07)	14 16.1 (0.26)	188 160.8 (4.59)
S lepr	3 2.9 (0.01)	6 7.7 (0.36)	9 8.6 (0.01	4 8.9 (2.69)	7 9.7 (0.76)	10 10.4 (0.01)	118 108.9 (0.77)
S parv	7 2.9 (5.57)	6 8.3 (0.62)	8 13.1 (1.98)	13 18.0 (1.38)	22 21.6 (0.01)	23 22.6 (0.01)	130 122.5 (0.46)
S fall	**27** 7.2 (54.10)	**92** 20.7 (244.73)	**98** 29.8 (155.98)	**57** 30.8 (22.19)	**60** 33.9 (20.05)	**63** 38.0 (16.39)	**226** 462.4 (120.88)
S pauc	**39** 13.2 (50.76)	**116** 33.9 (199.08)	**137** 45.2 (186.62)	**87** 45.7 (37.38)	44 45.0 (0.02)	50 39.4 (2.82)	**81** 331.6 (189.41)
P mala	1 8.7 (6.83)	**0** 23.7 (23.69)	**2** 29.3 (25.40)	**2** 30.0 (26.13)	**3** 33.6 (27.84)	**6** 30.6 (19.79)	**573** 431.2 (46.47)
H verv	**8** 1.1 (44.16)	**18** 3.3 (66.54)	**40** 4.8 (260.35)	**37** 5.4 (183.22)	**21** 5.9 (38.89)	8 6.6 (0.30)	**6** 111.0 (99.30)
S agam	0 0.7 -	1 1.9 (0.42)	5 3.2 (1.07)	5 3.7 (0.44)	**10** 4.2 (7.96)	5 4.8 (0.01)	135 142.6 (0.40)
V duli	**432** 3.4 (54288.32)	**394** 10.0 (14772.33)	19 16.5 (0.38)	**0** 23.3 (23.26)	**0** 29.7 (29.69)	**0** 36.6 (36.63)	**1** 726.5 (724.55)
V sara	1 1.0 (0.00)	3 2.5 (0.11)	2 3.3 (0.50)	2 4.2 (1.15)	5 5.1 (0.00)	6 6.0 (0.00)	78 74.9 (0.13)

Appendix 7 Percent area of the plot in 5 m distance regions from different species of focal adult trees in Plot 1. Area was calculated from a grid of points, each point being assigned to the nearest adult tree.

Focal adult species	distance region (m)					Total
	> 0 - 5	5 - 10	10 - 15	15 -20	> 20	
S joho	6.00	10.79	8.96	4.81	0.74	31.30
S arge	1.90	3.41	2.24	1.03	1.37	9.95
S lepr	1.71	2.73	1.82	0.38	0.00	6.64
S parv	1.20	2.52	2.12	1.20	0.16	7.20
S fall	1.05	2.30	1.65	0.60	0.01	5.61
S pauc	2.37	5.64	5.17	2.60	0.56	16.34
P mala	1.47	2.62	1.42	0.34	0.03	5.88
H nerv	0.78	2.03	2.28	1.98	0.38	7.45
S agam	0.24	0.18	0.61	0.08	0.00	1.11
V duli	0.40	0.83	0.61	0.58	0.03	2.54
V sara	1.07	2.34	1.71	0.87	0.08	6.07
Total	18.18	35.39	28.59	14.48	3.35	100.00
Cumulative %	18.18	53.57	82.16	96.64	100.00	